AUTUMNAL TINTS ON LAKE ERIE.

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1. *Rhus typhina.*
2. *Rhus Toxicodendron.*
3. *Ampelopsis quinquefolia.*
4. *Liriodendron tulipifera.*
5. *Pinus Strobus.*
6. *Thuja occidentalis.*
7. *Tsuga Canadensis.*

THE

NATURAL HISTORY OF PLANTS

THEIR FORMS, GROWTH, REPRODUCTION, AND DISTRIBUTION

FROM THE GERMAN OF

ANTON KERNER von MARILAUN

PROFESSOR OF BOTANY IN THE UNIVERSITY OF VIENNA

BY

F. W. OLIVER, M.A., D.Sc.

QUAIN PROFESSOR OF BOTANY IN UNIVERSITY COLLEGE, LONDON

WITH THE ASSISTANCE OF

MARIAN BUSK, B.Sc. AND MARY F. EWART, B.Sc.

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Growth and Construction of Plants

Plant-forms as Completed Structures.

another $\frac{8}{21}$ of the circumference; in the other case by $\frac{13}{34}$; and from this it follows that in the one instance there are twenty-one, and in the other thirty-four orthostichies.

If we place these actually-observed instances together, we have the series $\frac{1}{2}, \frac{1}{3}, \frac{2}{5}, \frac{3}{8}, \frac{5}{13}, \frac{8}{21}, \frac{13}{34} \ldots\ldots$

But the variety of the conditions on which the leaves are arranged is not exhausted by a long way. Although but seldom, still cases have been observed which can be placed together in the series $\frac{1}{4}, \frac{1}{5}, \frac{2}{9}, \frac{3}{14}, \frac{5}{23} \ldots\ldots$, and also in the series $\frac{1}{4}, \frac{2}{7}, \frac{3}{11}, \frac{5}{18} \ldots\ldots$ In all these series this very remarkable peculiarity occurs, that

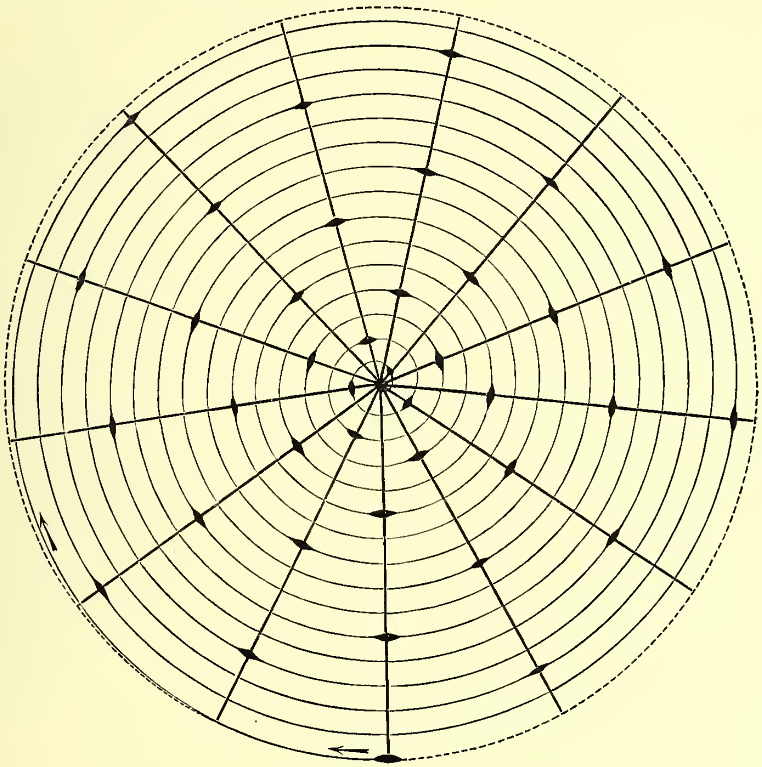


Fig. 100.—Plan of Five-thirteenths Phyllotaxis.

in each individual fraction the denominator is equal to the sum of the denominators, and the numerator is equal to the sum of the numerators of the two preceding fractions.

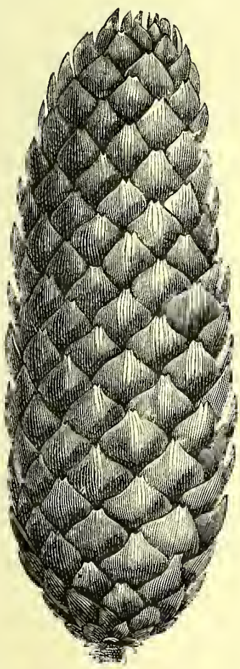
Moreover it must be here particularly mentioned that the divergence, by which the leaves following one another in age are separated in a horizontal direction, is the more difficult to establish the smaller it becomes. The one-third, two-fifths, and three-eighths arrangements are the most easily demonstrable on the full-grown shoots, although occasionally doubt arises as to whether the three, five, and eight orthostichies represent completely straight lines. But the demonstration of $\frac{8}{21}$ and the $\frac{13}{34}$ arrangements, especially in green herbaceous stems, is very difficult and uncertain.

There are only few plants on whose branches or axes several stories occur with twenty-one or thirty-four successive leaves in each. On the other hand, it happens that on many shoots, not even one story is completely formed, or in other words, that in more than a hundred leaves which project from the axis, no two are to be found situated quite vertically above one another, and consequently, in these cases, rectilineal orthostichies are out of the question. In many fir-cones, for example, rectilineal lines are sought for in vain, and it is impossible, even approximately, to estimate how many leaves are included in one story. It has been also conjectured that in such cases the leaves of a story are innumerable, and if so, the fraction by which such a system of leaf-insertion would be represented would be an absurd figure.

In such shoots it is anything but easy to establish the successive ages of the leaves, that is, to number them in their proper order of development, especially when the leaves are thickly crowded together. This becomes the more difficult when the leaves on such very crowded axes arrange themselves in spiral series, or lines which are much more apparent to the eye than the lines of development or genetic spirals. These spiral series, which are seen on shoots of many succulent plants (*Sedum, Sempervivum*), on species of *Pandanus* and *Yucca*, on the branches of lycopodiums and conifers, and especially also in the inflorescence of crucifers and the cones of many firs, of which a pine-cone, represented in fig. 101, may be taken as an example—these series are called *parastichies*. They may be utilized in order to ascertain which leaves succeed one another in age, thus—by first of all ascertaining how many such parallel spiral lines ascend to the right, and how many to the left on the axis examined. In a pine-cone, for example (see illustration below), eight such lines or parastichies are seen to ascend in a somewhat sharply oblique direction to the left, and five to the right in a rather less sharply oblique direction. In order to find out which leaves succeed one another in age, the lowest leaf is called 1, and the numbers 8 and 5 are used in the following manner. The leaves of those steep parastichies, on the left adjoining 1, are numbered by additions of 8 respectively, 9, 17, 25, 33, 41, &c. The leaves of the less steep parastichies on the right, which adjoin 1, are numbered, on the other hand, by additions of 5 respectively, 6, 11, 16, 21, 26, &c. The numbering of the other parastichies is then easily completed by subtractions and additions of the numbers 8 and 5, and the numbers so obtained represent the successive ages of the leaves on the cone. This somewhat complicated arrangement may be best demonstrated by imagining the surface of a leafy, almost cylindrical axis, *e.g.* of a pine-cone, to be slit up longitudinally, rolled out flat, and extended so that all the leaf-scales lie in one plane, as represented in the plan illustrated in the right-hand figure opposite.

Naturally the most lively interest has been aroused at all times by the geometrical ratios of phyllotaxis here generally reviewed, and it could not fail to follow that the most diverse speculations should have been connected with them. This is not the place to consider these in detail, but in so far as the remarkable and actually existing conditions of the geometric arrangement of the leaves have a

significance in the life of the plant, the attempts to explain them must not be passed over. First of all, it must be pointed out that the number of orthostichies, *i.e.* of the leaf-members of a story, as well as the number representing the circuits made by the genetic spiral in each story, is connected with the extent of the horizontal divergence between consecutive leaves. In order to make this clear, let us draw a spiral line on the surface of a cone, as shown in fig. 99, and let us place dots on this line at regularly recurring intervals. The length of the interval between the dots is quite immaterial, it is only of importance that the successive dots shall remain separated from each other by the distance originally fixed upon.



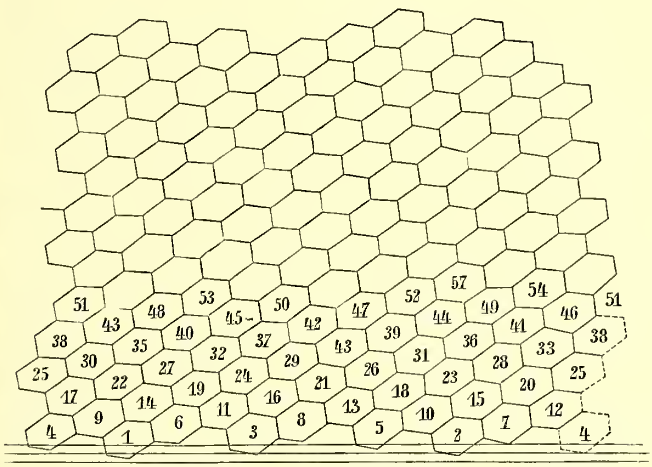


Fig. 101.—Parastichies of a Pine-cone

The eight parastichies turning steeply to the left, start from the points 1, 6, 3, 8, 5, 2, 7, 12; the five turned less steeply to the right, from the points 4, 1, 3, 5, 2.

Suppose that the dots are placed on the spiral line at intervals of $\frac{1}{10}$ of the circumference of the circle (36°), then in each revolution of the spiral there will be 10 dots, separated by equal distances from one another. With the tenth $\frac{1}{10}$, however, the spiral line has completed the circuit of the cone, *i.e.* of the axis. The eleventh dot lies vertically above the first dot, and with it begins a new revolution and a new story. On such a stem ten orthostichies would necessarily be produced, and if we substitute actual leaves for the dots, the phyllotaxis will be represented by $\frac{1}{10}$. As another example, let us place the dots on the spiral line at horizontal distances of $\frac{2}{7}$ of the circumference. How will the dots then be arranged? Dot 2 is $\frac{2}{7}$ of the circumference of the circle from dot 1; dot 3, $\frac{2}{7}+\frac{2}{7}=\frac{4}{7}$; dot 4, $\frac{2}{7}+\frac{2}{7}+\frac{2}{7}=\frac{6}{7}$; dot 5, $\frac{2}{7}+\frac{2}{7}+\frac{2}{7}+\frac{2}{7}=\frac{8}{7}$ of the circumference from dot 1, measured along the genetic spiral. Dot 4 is not quite vertically above dot 1, and dot 5 lies beyond it, neither of the two, therefore, coming exactly above 1. More dots are now placed at the same intervals on the second revolution of the spiral line; first dot 6, which is $\frac{10}{7}$, then

dot 7, which is $\frac{12}{7}$, and, finally, dot 8, which is $\frac{14}{7}$ of the circumference from dot 1 along the genetic spiral. Dot 8 is found to lie exactly above dot 1, and here the second revolution of the spiral line is completed. This is the termination of the first story, and with dot 8 a new one commences. On a stem whose leaves are distributed in the same way as the dots in the example just described—any two of which are always separated from one another by $\frac{2}{7}$ of the circumference in a horizontal direction—seven orthostichies will be produced, and the genetic spiral, *i.e.* the line which connects the leaves consecutively following one another according to their age, will make two revolutions round the stem. Such an arrangement would be designated as a two-sevenths phyllotaxis. From these examples it follows that a definite phyllotaxis corresponds to each horizontal divergence between leaves following one another in age, whatever this may be, as long as it only remains constant. The divergence measured along the circumference of the stem may be large or small. Finally, there will be an equal distribution of leaves around the stem, and they will project at equal horizontal distances in as many directions as are given by the denominator of the fraction representing the divergence. But the spiral line which connects all the leaves represented by the denominator with one another will make as many circuits round the stem as the number constituting the numerator of the fraction. In other words, the extent of the horizontal divergence always gives us the phyllotaxis. The denominator of the fraction is equal to the number of orthostichies, and the numerator is equal to the number of revolutions made by the genetic spiral in each story.

The observation already alluded to above, according to which those fractions by which the phyllotaxes actually found in plants may be expressed as members of a definite series, must now be considered further. It has been found that the horizontal divergences between consecutive leaves respectively form part of a continued fraction of the form

$$\cfrac{1}{z + \cfrac{1}{1 + \cfrac{1}{1 \ldots\ldots,}}}$$

in which z is a whole number. If for z we substitute the number 1, the successive parts of the fraction will give us the series $\frac{1}{2}, \frac{2}{3}, \frac{3}{5}, \frac{5}{8}, \frac{8}{13}, \frac{13}{21}, \ldots\ldots$ If $z = 2$, the series $\frac{1}{2}, \frac{1}{3}, \frac{2}{5}, \frac{3}{8}, \frac{5}{13}, \frac{8}{21} \ldots\ldots$ is obtained. If $z = 3$, the series $\frac{1}{3}, \frac{1}{4}, \frac{2}{7}, \frac{3}{11}, \frac{5}{18}, \frac{8}{29} \ldots\ldots$, and if $z = 4$, the series becomes $\frac{1}{4}, \frac{1}{5}, \frac{2}{9}, \frac{3}{14}, \frac{5}{23}, \frac{8}{37} \ldots\ldots$ It is remarkable here that among all the phyllotaxes, those represented by the numbers $\frac{1}{2}, \frac{2}{3}, \frac{2}{5}, \frac{3}{8}, \frac{5}{13} \ldots\ldots$ occur most frequently, while phyllotaxes belonging to the other above-quoted series are only occasionally met with. Thus, as a matter of fact, the series occurs oftenest in which 2 is substituted for z. The advantage offered by the series produced from this number has been explained in this way: by it, on the one hand, phyllotaxes are produced by which an equal distribution of the leaves is obtained by the smallest possible number in each story; and, on the other hand, phyllotaxes again in which leaves may project from the stem in very many different directions.

The reason why each species of plant arranges its leaves, even while in the

bud, in the most advantageous manner, quite independently of external influences, without the knowledge, so to speak, of the conditions to which its foliage-leaves will be exposed in the future, can only be explained by the specific constitution of its protoplasm. Just as crystals are formed from the aqueous solution of a salt which, according to the nature of the salt, are sometimes six-sided, sometimes three-sided, whose surfaces are always the same in outline, and whose edges always form exactly the same angles, so bands, bars, and partition-walls arise in the growing cells, by which these cells become articulated and divided; and the shape and position of these intercalated walls and their geometrical ratios are no less definite in the most diverse plant species than are the surfaces of the crystals arising from the salt solution. But that which applies to the plan of construction of the individual cells must also apply to the plan according to which a group of cells—a tissue, a growing shoot, a stem with its leaves, even the entire plant—is constructed. The position on the circumference of the stem at which a leaf originates is certainly not determined by chance, but is based upon the molecular constitution and composition of the protoplasm of the species of plant in question; and if the leaves on an oak-branch always arrange themselves in $\frac{2}{5}$ phyllotaxis, the constancy of the arrangement is neither more nor less remarkable than the constancy of the size of the angles in an alum octahedron.

It should be noted here, in this connection, that the geometrical arrangement of the cells in simple elongated tissues, easily accessible to observation, is exactly similar to the arrangement of the leaves on stems. For example, the cells on the hair-like stigmas of grasses follow the one-third arrangement very beautifully. A connection between the geometrical arrangement of the cells at the apex of a growing stem, and the geometrical arrangement of the leaves on the same, may now also be considered. A group of cells is formed out of each cell at the growing point of the stem by the repeated intercalation of division-walls. If the position of these dividing cells is geometrically defined, and if the partition-walls resulting from their division assume definite directions in each species of plant, then the arrangement of the cell-groups produced from these cells which build up the stem must also be geometrically defined. Supposing now that from each of these groups of cells which build up the stem a leaf arises, then the distribution of the leaves on the circumference of the stem will be only a repetition of the distribution of the cells at the growing point of the stem. In the simplest of all leafy stems, in that of a moss-plant, this relation is noticeable enough; but in plants of more complicated construction it is not so easily demonstrated. In these the constancy of the geometric ratios of the cells at the growing point is beset with many difficulties, and the groups of cells produced from them are also much displaced and distorted. Nevertheless in each form of plant a uniform plan of construction very probably exists; and it may be taken for granted that in each species the arrangement of the atoms in the protoplasm, the arrangement of the cells, and the arrangement of the leaves, are based upon the same symmetrical construction.

Indeed, even the displacements and torsions of the cells which occur in leafy

stems without doubt take place according to rule, although they may be in part due to external causes. Numerous comparative observations have shown that the building, and especially the lengthening of the growing stem, does not always follow the direction of a straight line; that, rather, a spiral torsion of the cells and tissues not infrequently occurs, so that the idea that such a stem by its growth bores its way through the air is quite justified. This does not, indeed, refer to the twining of the stem, which will be discussed later, but to the torsion of the tissue mass of a straight stem which remains straight after the torsion has been effected, and which may best be compared to the twisting of a bundle of rectilineal strands to form a string. In every bud from which a leafy branch arises, the points of origin of the leaves may be seen on the periphery of the still very short conical axis; frequently, also, the shape and outline of the leaves are perceptible, and the position and divergence of the leaf-insertions can be geometrically established. If the axis has elongated, and an extended branch been produced from the bud, the arrangement displayed by the fully-formed, displaced leaves does not always coincide with that in the bud. The phyllotaxis has become altered by reason of the pressure which the individual groups of cells exercise on one another in their increase in length and breadth, and in consequence of displacements connected with these pressures, *i.e.* torsions arise. If the torsion is restricted to one portion of the stem only, an actual transition of one phyllotaxis into another is seen, and occasionally it is very pronounced.

In order to make clear the alterations arising in this way, it is only necessary to remove the leaves from a herbaceous leafy stem, to hold it by the two ends, and to twist it as a bundle of threads might be twisted into a string. The points of insertion of the leaves are thus mutually displaced, parastichies are formed from the orthostichies, and new, often very complicated, leaf-arrangements come into view. The alterations produced by the torsion of the stem may also be rendered evident by a consideration of fig. 102. Let us suppose that the black dots on the three thick lines of the young conical stem, horizontally projected in this illustration, indicate leaf-positions which are separated from one another by a distance of $\frac{1}{3}$ of the circumference of the circle (120°). Suppose now that the stem has undergone a torsion as it lengthened, which is quite definite and equally distributed over all portions of the stem. Each portion of the stem between two consecutive leaves, following one another in age, is twisted through, say $\frac{1}{15}$ of the circumference (24°), and in consequence of this the divergence of the leaves is no longer $\frac{1}{3}$ of the circumference, *i.e.* 120°, but $120° + 24° = 144°$, or, as much as $\frac{2}{5}$ of the circumference. By reason of this the points of origin of the leaves come to lie in the positions indicated by the thinner lines, and a two-fifths is produced from a one-third phyllotaxis. In the same way the three-eighths arises from the one-third phyllotaxis if the consecutive dots are displaced $\frac{1}{24}$ of the circumference (15°) by the torsion, and the horizontal divergence no longer amounts to $\frac{1}{3}$ of the circumference, but to $\frac{3}{8}$. The one-third becomes changed into the one-half phyllotaxis if the second leaf of a story, which in the bud was separated

from the first by $\frac{1}{3}$ the circumference, in consequence of the torsion of the growing stem, is displaced about $\frac{1}{6}$ the circumference (60°); that is to say, exactly so much that it is now separated from the first by half the circumference (180°). This particular alteration can be very well seen in the developing branches of beeches, hornbeams, hazels, and many other trees and shrubs. In the buds the leaves have a one-third arrangement, in the fully formed, now woody branches the phyllotaxis appears to be one-half. Since, as a rule, amongst buds, the simplest cases, especially

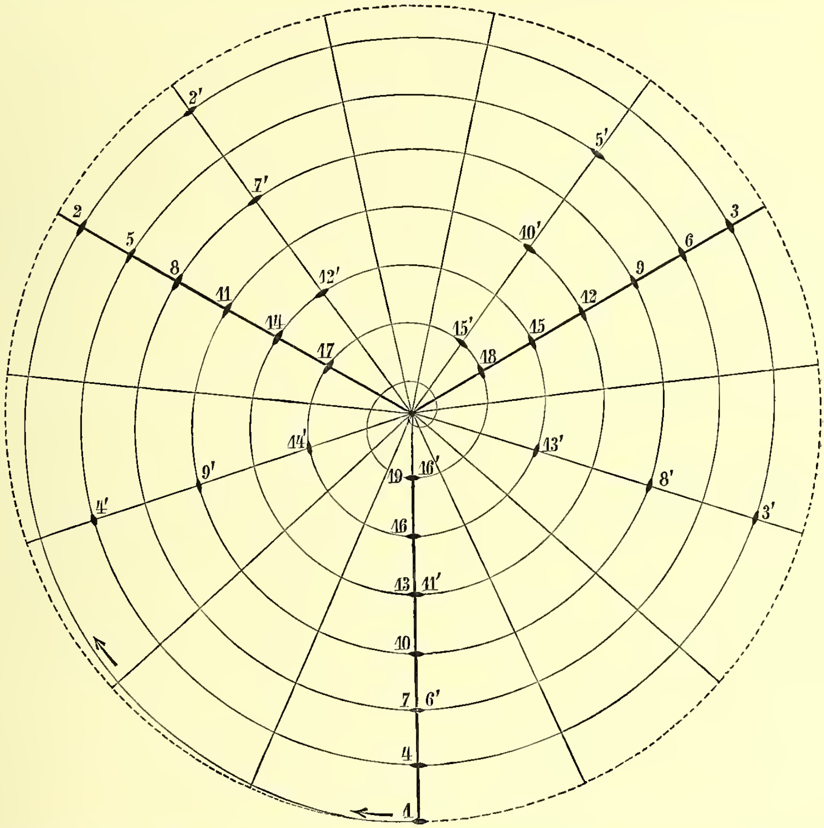


Fig. 102.—Displacement of the leaf-positions in consequence of torsion of the stem.
Transformation of the one-third into the two-fifths phyllotaxis. Dot 2 is displaced by torsion to 2′; dot 3 to 3′, &c.

the one-third arrangement, are most frequently observed, it appears probable that the number of original phyllotaxes is really only very small, and that complicated leaf arrangements, which are represented by fractions whose numerator consists of two figures, frequently are produced by torsion of the individual parts of the stem during their growth. It still remains to point out here that the phyllotaxis becomes the more complicated, the less the amount of torsion undergone by an internode, which is, indeed, evident from the preceding representation. It is also worthy of note, that in plants whose foliage-leaves originate 2, 3, or more together at the same height on the stem (which therefore possess whorled leaves), such torsions of the internodes, and alterations of the phyllotaxis dependent upon them, very frequently occur.

RELATION BETWEEN POSITION AND FORM OF GREEN LEAVES.

Now that the distribution of the green leaves on the surface of the stem has been generally described, it is possible to discuss the relation of the phyllotaxis to the length and breadth, as well as to the shape and direction, of the leaf-blades.

If a small leafy moss-plant, or a huge densely-leaved tree be examined, it will always be found that the number of orthostichies on the straight stems becomes smaller as the leaf-blades become broader. If the leaf-blades are circular, like those of the Judas Tree (*Cercis Siliquastrum*), or if they are broadly ovate or cordate, being broadest at the base, like those of limes and elms, or if they are not perhaps borne on very long petioles, *i.e.* like those of the Aspen (*Populus tremula*), then they pass down the stem in two lines, thus displaying a one-half phyllotaxis. If the leaf-blades are broadly elliptical, and therefore broadest about the middle, and also have but short stalks, like those of beeches, alders, and hazels, then they are arranged regularly in three rows on the erect branches and display a one-third phyllotaxis. If the leaves are obovate, *i.e.* broader at the top than at the base, and at the same time have only short stalks, as, for example, those of oaks, then they are arranged in five lines, according to the two-fifths phyllotaxis. If they are lanceolate or oval, like those of the Almond-tree, they usually have the three-eighths phyllotaxis; and finally, the narrow linear leaves on the twigs of the *Genista tinctoria*, as well as the long narrow leaves on the stems of the Golden-rod (*Solidago*), are regularly arranged in a five-thirteenths phyllotaxis. In the mosses the same relations hold good; the broad leaves of the *Mnium* species display the one-third; the elliptical and oval leaves of many earth-mosses (*Barbula*) the two-fifths; and the narrow linear leaflets of polytrichums the three-eighths, five-thirteenths, and more complex phyllotaxis. This connection between the breadth of the leaf-blade and the number of rectilineal leaf-rows on the erect stem is very noticeable even in members of the same genus, and in this respect perhaps no genus is so instructive as the willow. There are willows with circular, elliptical, oval, and narrow linear leaves, and in these it can be plainly seen that the number of orthostichies increases in proportion as the leaves become narrower. *Salix herbacea* with circular leaves has a one-third, *Salix Caprea* with elliptical foliage a two-fifths, *Salix pentandra* with lanceolate foliage a three-eighths, and *Salix incana* with linear leaves a five-thirteenths phyllotaxis.

If we take erect branches from each of these willows, placing them all together, and look down upon them from above, we see how the three, five, eight, and thirteen rows of leaves radiate out from their respective axes. But it is also plainly evident that in each case the neighbouring rows so adjoin one another as to leave no gaps between them, so that the space round the stem may be utilized to the greatest possible extent. In one case, therefore, we have three rows of very broad leaves, in other cases five or eight rows of moderately broad leaves, and again in another instance thirteen rows of very narrow leaves.

All the rows of leaves, whether there be three, five, eight, or thirteen of them, are equally illumined by the sunbeams which strike them from above in the direction of the axis of the branch; no row throws another into the shade, and only the upper individual members of a row standing above one another can deprive the lower members of light. But even this shading is avoided, chiefly by the adaptation of the length and direction of the foliage-leaves to the height of a story.

If the stories are low, so that the consecutive leaves of a rectilineal row are separated only by short distances, then the leaves are short; if the stories are high, then the leaves are long; the length is always so arranged that the sunbeams can penetrate into the space between every two leaves of a row, and can, so to speak, illuminate the interior of the story.

It should be remembered here that the sun does not shine down vertically upon branches having an upward direction, that its rays, even at the equator, fall obliquely in the morning and evening, and at these times illuminate the space, bounded above and below by two consecutive leaves of a row, just like the rays of the rising and setting sun which enter a room through the window. But this does not say that no leaf is thrown into the shade throughout the entire day. This would be impossible, from the fact that the sun's rays at each hour of the day fall at a different angle on the plants which remain firmly fixed and immovable in the soil. The leaves of one side are partially shaded in the morning, and those of the other side in the afternoon; or they are only illuminated by diffuse light; and the upright stem, which is set round about with projecting leaves, must necessarily shade a portion of them for a short time during the day. But these shadows, like the dark lines thrown by the gnomon of a sun-dial, must continually move forward with the sun, and only remain in one place for a little while.

The entrance of the sun's rays between the leaves situated above one another is, moreover, materially influenced by the direction of the leaf-blades. A leaf projecting obliquely upwards from the stem, with its midrib in the plane of the incident rays, will not at any hour of the day deprive its lower-placed neighbour of too much light, or at any rate to a much less extent than will a leaf whose blade is extended horizontally or sloped a little in an outward direction, and which presents its broad side to the incident sunbeams. This explains a phenomenon which is seen very often in annual and biennial composites and crucifers with straight, erect stems. The lowest leaves of these plants form a right angle with the axis of the stem, and lie with their broad surfaces on the soil, completely covering a larger or smaller area. These can obviously not take away the light from any other leaves of the same plant. The leaves inserted higher up the stem are, on the other hand, no longer extended horizontally, but rather in an upward direction, and form an angle with the stem which is less than a right angle; and the highest leaves even approach the upright, their midribs lying in the plane of the incident noonday rays.

In accordance with this adjustment, an alteration of the dimensions, particularly of the length of its leaves, may be observed at different heights of an erect thickly-

leaved stem. The lowest leaves originating next the soil are the longest; the leaves next above these are, on the other hand, visibly shorter, and often in the region of the flowers are changed into insignificant scales closely applied to the stem. It can easily be seen in every plant of the Shepherd's Purse (*Capsella Bursa pastoris*), on every mullein (*Verbascum*), and every hawkweed (*Hieracium*), that such small upwardly-directed leaves cannot injure by overshadowing the leaves growing below them either in the same or in adjacent rows.

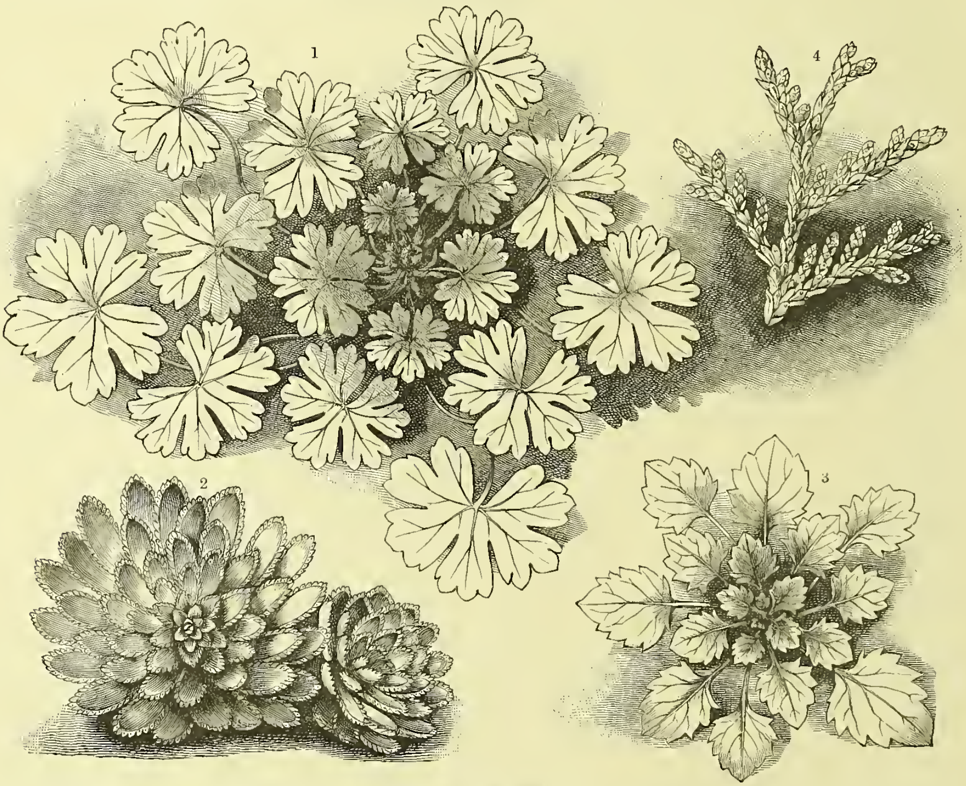


Fig. 103.—Leaf-mosaic.

[1] Leaf-rosettes of a Crane's-bill (*Geranium Pyrenaicum*) seen from above. [2] Leaf-rosettes of a Saxifrage (*Saxifraga Aizoon*). [3] Leaf-rosette of a Bell-flower (*Campanula pusilla*) seen from above. [4] Adpressed scale-like leaves on the twig of an Arbor Vitæ (*Thuja*).

Many plants produce within a year, at the ends of their upright shoots, a large number of leaves which radiate out from the stem with very small horizontal divergencies, standing close above one another, and forming a so-called *rosette.* In order that all the leaves of such a rosette may receive an equal proportion of light, it is absolutely necessary that the upper leaves should be considerably shorter than the lower. And in all rosettes this is actually the case. However, some very interesting modifications are to be seen. In rosette-forming succulent plants (*e.g.* *Echeveria* and *Sempervivum*), and in many saxifrages (*Saxifraga*), of which a species (*Saxifraga Aizoon*) is represented in fig. 103 [2], the leaves are tongue-shaped or spatulate, and about twice as broad near the further end than at the point of

insertion upon the abbreviated axis. It is unavoidable that the narrower, proximal halves of most of the leaves should be covered by the leaves above and fail to receive sufficient light. But these covered portions are always destitute of chlorophyll, and so have no need of direct sunlight. The distal halves, on the other hand, which display green tissue, can by this arrangement be all well illumined simultaneously by the sun. In many other instances the increase in length is only found in the leaf-stalks of the lower leaves of the rosette. These increase in length, that is to say, until the blades borne by them are moved out of the shadow of the

Fig. 104.—Formation of a Leaf-Mosaic by the lengthening (relative shortening) of the Leaf-stalks.

[1] Small-leaved Balsam (*Impatiens parviflora*). [2] Green Amaranth (*Amarantus Blitum*). [3] Thorn-apple (*Datura Stramonium*).

leaves above. This is the case, for example, in the leaf-rosettes of *Geranium Pyrenaicum*, represented in fig. 103 [1], and in the leaf-rosettes of the dainty little bell-flower (*Campanula pusilla*, fig. 103 [3]) growing on the débris-covered slopes of the sub-alpine regions. In these bell-flowers the great difference in shape between the rosette-leaves and those clothing the flower-stalk is worthy of remark. The latter, which spring at an acute angle from the stem, are narrowly lanceolate, and have very short stalks, while the lower rosette-leaves, extended flatly over the soil, have long stalks, and possess a broad, ovate blade. It is no disadvantage to the leaf-stalks, which have no chlorophyll, if they are placed in the shade. But by this arrangement all the broad, green leaf-blades are well illumined, and this applies also to the more loosely-arranged, upwardly-directed, narrow leaves of the stem.

The leaves of many plants with elongated, erect stems, though at a moderate distance from one another, are often arranged in a kind of rosette, and this is effected by the stalks of the lower leaves becoming considerably longer than those of the leaves situated near the apex. This condition is especially seen in the marsh-plants, whose flat leaves lie on the surface of the water, viz. in *Villarsia, Hydrocharis, Polygonum amphibium,* many species of the genus *Callitriche,* and many water-inhabiting Ranunculaceæ. Among terrestial plants this grouping of the leaves is displayed particularly by many Amarantaceæ. In the erect shoots of *Amarantus Blitum,* illustrated in fig. 104 [2], the stalks of the lower leaves of a row are six, seven, or eight times as long as those of the upper leaves. In this way the whole of the green foliage of the plant can be spread out almost at the same level without any one overshadowing another.

In plants with elongated stems, the mutual encroachment of the numerous leaves situated one above another is also prevented by a further arrangement. We mean the development of the leaves in the form of green scales adpressed to the stem, as observed in so many conifers, *e.g.* in the twigs of a *Thuja,* as represented in fig. 103 [4]. It is true that only the under surface of the small leaflets can meet the sun's rays, but the effect is the same as if only the upper side had been illumined, as, for example, in those leaves projecting from the erect stems at a right angle, or inclined with their apex towards the soil. Since the small green leaflets clothing the stem are arranged side by side, like the tiles on a roof, and the greater portion of the under surfaces remains uncovered by the adjoining leaves, no mutual withdrawal of light can be said to occur, in spite of the crowded arrangement.

The arrangements of green leaves as just described relate exclusively to instances in which the blade of the leaf is neither lobed nor compound, but entire. A leaf can deprive another, originating a little below it from the erect stem, having the same shape and size, and the same inclination, either entirely or almost entirely of the sun's rays, only when entire. A leaf whose green lamina is sinuous, lobed, divided, or incised, will always allow abundant sunlight to pass between the lobes and segments on to the leaves below; and the deeper, wider, and more numerous the incisions producing the separation into lobes and segments, the more will be the light passing through. Of course strips of shadow will be formed, but they move their position during the day, remaining in one spot only for a short time; and it would appear that such a rapidly passing shadow has anything but an injurious effect on the green tissue. From this it follows that in plants with divided foliage, the adjustment described previously for the case of entire leaves is superfluous. As a matter of fact, in plants whose foliage-leaves have a much-divided blade, the fully-grown upper and lower leaves are of equal length; they all project from the erect stem at the same angle, and the stem is, generally speaking, never clothed with lobed or pinnate leaves closely covering it like scales. In the Fennel and Dill, in Chamomile, Larkspur, and species of the genus *Adonis,* the lower and upper leaves of the stem are so alike that it is hardly possible to say whether an isolated

single leaf had been plucked from the lower or upper part of the stem. Only the lowest leaves of all, whose shadow falls on the ground and not on neighbouring leaves, are divided into broader sections; the others are equally divided and project at equal intervals round the stem. While the Mullein, with its entire foliage-leaves, rapidly diminishing in size towards the summit, presents a pyramidal appearance from a distance; the Fennel and Larkspur, whose finely-divided leaves are similar all along the stem, rise up like cylindrical columns. In other words, if the extreme outer point of all the leaves of the last-named plants are connected together in a surface, this will take the form of a cylinder. Only when projecting, divided leaves are crowded above one another on a very short stem, as, for example, in ferns, and where the plants are growing in shady places where the light is very scanty, it happens that the lower leaves are raised above the upper in order not to miss too much of the enjoyment of the light.

The perforation of the leaf-blades, which is observed, though but seldom, in many aroids, has now to be considered. The best known in this respect are the Brazilian *Monstera egregia*, and the *Tornelia fragrans*, illustrated in fig. 96, which has also been called by gardeners, in consequence of the gaps in the leaves, *Philodendron pertusum*. The circular or elliptical holes do not originate late on in the leaf-blade, but can actually be seen when the small and undeveloped leaves are yet folded. They are always formed on the upper leaves of older plants; the leaves of younger, shorter specimens do not possess them. This circumstance suggests that the holes have the same significance as that previously assigned to the deep incisions and clefts between the leaf-lobes. They are chinks in the broad upper leaves whose shadow extends over a large area, through which a portion of the obliquely falling rays of light can reach the more deeply situated leaves. The peculiar notches in the blades of certain leaves of the Black Mulberry-tree (*Morus nigra*), as well as of the Japanese Paper Mulberry (*Broussonetia papyrifera*), may be explained in like manner. They are only found on the upper leaves of a branch, and are best seen on the erect slender shoots which spring from the base of old trunks. Sometimes, in these highest leaves, only one half has an incision extending almost as far as the midrib; sometimes again both halves are provided with deep clefts; in the highest shoot-leaves of the Black Mulberry-tree the blade is often divided up into fairly narrow segments by several incisions on both sides. If such developing shoots, crowded closely together, are observed at mid-day, when they are directly illumined by the sun, the shadow of the upper leaves can be seen sketched out on the leaves below, but to each incision and indentation of a leaf at the apex, a patch of light corresponds on the leaf-surfaces in the stories next below. Suppose now that the holes above had been closed; immediately it would become darkened underneath, the spots of light which continually move according to the position of the sun from place to place and from leaf to leaf would be wanting, and the activity of the green tissue in the leaves of the lower region would be to some extent impaired.

It was not without reason that in each separate instance hitherto described, emphasis has been laid on the fact that the foliage-leaves in question were situated on erect stems, and this must again be particularly pointed out here. The conditions on horizontal branches are entirely different, and what is suitable for one is not always fitted to the other. It is easy to make this evident. It is only needful to bend down an erect leafy maple-branch until it becomes horizontal, and it will immediately be seen that the surfaces of the leaves on the branch assume a position and direction very different from their previous attitude. The narrow side, instead of the broad side as previously, is directed towards the incident light, and the leaves now stand above one another which formerly stood opposite at the same height from the ground. If the arrangement of the foliage-leaves on the erect branch was previously suitable and beneficial, the contrary is now the case. Such alterations in the position of the foliage-leaves or shoots and branches of plants, however, occur not only by way of exception, but very frequently. It signifies the less that strong winds bend and incline the leaf-stalks and twigs, since this alteration of position is, as a rule, only of short duration, and when the storm is past, the former position is again taken up. The pressure which snow exerts on plants in regions where in winter the fall is heavy, is, indeed, of more importance, and can produce alterations in the position of the twigs and branches which are of longer duration. But most important of all is the fact that perennial plants add a new portion to the end of their shoots every year, that they always develop each year new sprouts above those already existing, and not only at the apex, but also from buds which arise laterally on the branches. Let us observe a young maple whose topmost branch terminates in three buds. Twigs issue from the three buds with the renewal of activity in the spring; the central bud grows directly upwards, the two lateral rise obliquely; all three are thickly leaved, and the foliage of the three twigs covers over and shades three, four, perhaps ten times as large a space as the pair of leaves from whose base the buds had developed in the previous summer.

Now, above the centre of the maple as it was in the previous year, what may be termed a new richly-leaved and thickly overshadowing little maple-tree grows up. That mutual consideration, which is otherwise observed by members of the same plant, and which was described earlier, here ceases. The leaves of the topmost shoot are, of course, so arranged that no mutual injury is done; but very little attention appears to be paid to the leaves below, as little perhaps as to the lower grasses and herbs which grow under the maple-tree on the ground.

But what are the branches to do which spring from the buds in the centre of the maple-tree under consideration? If they take the same direction as the branches at the extreme summit, they will come into the area of the dark shadows thrown by the numerous broad leaves of the top branches. They are, therefore, compelled to take up another direction if their leaves are not to perish from want of light. And, as a matter of fact, this is what they do. They arrange

Fig. 105.—Fir Trees.

themselves, that is to say, more or less horizontally, and increase in length in this direction until their leaves project outside the shadow of the topmost leafy branches, so that they may be able there to catch the sunlight. All this is observed not only in maples, which have been selected as examples, but in all richly-leaved trees and shrubs; the topmost branches are directed vertically upwards, the next lower rise obliquely, those still lower extend horizontally, and the lowest of all frequently even incline earthwards. The twigs of the older, lower branches which have grown out beyond the shaded area often again try to rise, and assume a direction which is almost similar to that of the highest branches at the summit. Such branches and twigs then display a curvature which is like a Roman ∿ lying sideways. Oaks and horse-chestnut trees furnish striking examples of this. The phenomenon is shown still better in firs (see fig. 105), in which the twigs springing from the lowest branches frequently rise almost vertically. This last circumstance is also of interest in so far as it indicates that it is not only the weight of the leaves which brings about the altered direction of the branching, but that it depends also on other conditions, to be discussed later on.

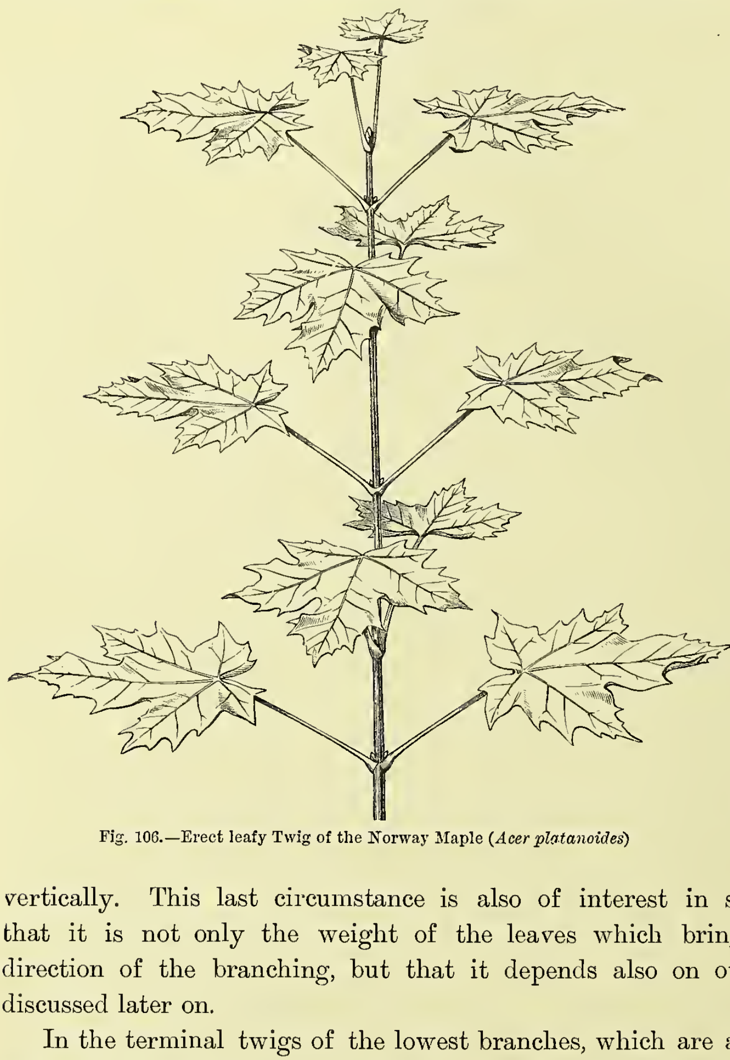


Fig. 106.—Erect leafy Twig of the Norway Maple (*Acer platanoides*)

In the terminal twigs of the lowest branches, which are again turned upwards, the same distribution and direction of the leaf-blades as are displayed by the erect twigs of the summit will naturally be resumed; but it is not so in the case of those twigs which retain a horizontal direction, or whose summits are even inclined towards the ground. Suppose that the maple-twig, which is illustrated here, has not grown from a central bud of the summit, and does not rise vertically upwards, but that it has been developed from an older, lower branch, and is extended

almost horizontally. If the surface of the foliage-leaves on the horizontal twig retains the same direction as those on the erect twig here represented, this will be the most disadvantageous position imaginable with regard to the incident light. It is urgently necessary that they should alter this position and again arrange themselves suitably. This rearrangement of the leaf-surfaces proceeding from the horizontal twigs is carried out, and, indeed, in four different ways. Either an adequate twisting of the internodes is effected; or a twisting of the leaf-stalks occurs; or the leaf-stalks do not undergo actual torsion, but their inclination to the leaf-blade becomes altered; or, finally, individual leaf-stalks lengthen to an extraordinary extent; so that the blades borne by them are carried far beyond

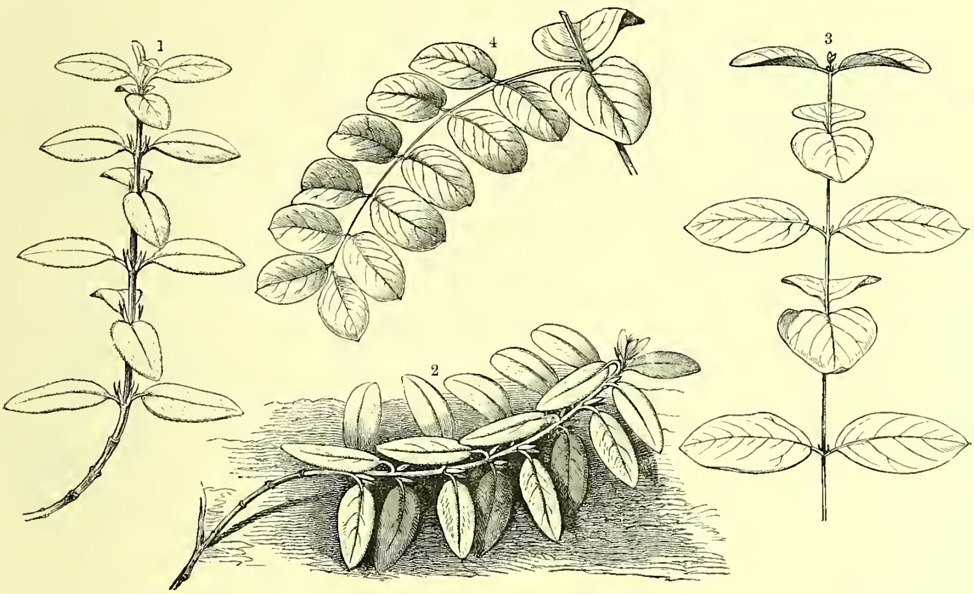


Fig. 107.—Twisting of Internodes and Leaf-stalks.

1 Erect twig of the large-flowered Rock Rose (*Helianthemum grandiflorum*). 2 Procumbent twig of the same plant. 3 Erect twig of *Diervilla Canadensis*. 4 Twig of the same plant, bent downwards.

their neighbours. It naturally very frequently happens that these alterations are also combined in many ways.

The first instance, the twisting of the internodes, may be observed in hazels beeches, and hornbeams, and especially in trees, shrubs, lianes, and bushes with decussating short-stalked leaves, as for example in *Cornus* and *Thunbergia*, in *Lonicera* and *Diervilla*, in *Androsœmum* and *Hypericum*, in *Thymus* and *Vinca*, *Coriaria myrtifolia*, *Gentiana asclepiadea*, and innumerable others. Fig. 107 [3] represents an erect twig of *Diervilla Canadensis*. As soon as such a twig develops no longer upwards, but horizontally, a twisting of 90° takes place in each internode, and the consequence is that the surfaces of all the pairs of leaves take up the same position towards the sun, as shown in fig. 107 [4]. The leaves are now no longer arranged in four, but in two, rows.

Very often twisting of the petioles goes hand in hand with that of the inter-

nodes. The torsion of the leaf-stalks of the Judas Tree (*Cercis Siliquastrum*), where this alone occurs, *i.e.* without a simultaneous twisting of the internodes, is particularly striking. The leaves of the plant, as can be seen on the erect twigs, and especially well in the suckers, are arranged in the one-half phyllotaxis, *i.e.* in two rows. The leaf-blades on the erect branches are parallel with the ground. If a sucker be cut off and held horizontally, all the leaf-laminæ will be directed at right angles to the earth. One might perhaps expect that they would also assume this direction if the twig had grown horizontally. Anything but that, however. The stalks of all the leaves twist round instead, until the laminæ, or blades they bear, are again placed in a direction parallel with the ground on the horizontal branches, and the result is that the leaves on all the branches of

Fig. 108.—Horizontally growing leafy twig of the Paper Mulberry-tree (*Broussonetia papyrifera*).

the Judas Tree, whether erect, oblique, horizontal, or inclined towards the earth, always present the same attitude to the incident light.

The third case, the alteration in the inclination of the blade to the leaf-stalk, which, on the whole, is but seldom met with, is represented in the best known example, the cursorily mentioned Japanese Paper Mulberry (*Broussonetia papyrifera*) in fig. 108. In this plant the leaves are decussate, *i.e.* arranged in four rows, each pair of leaves being inserted at the same level, and the successive pairs alternating at right angles. In erect twigs, therefore, they display the arrangement seen in the twigs of maple (see fig. 106) or of *Diervilla* (see fig. 107[3]). The following alteration, however, is seen to occur in the horizontal branches of the lower boughs of the Paper Mulberry. In each pair of leaves the leaf-stalk of one leaf becomes parallel to the surface of the ground, and lies in the plane of the blade it supports, which is also almost horizontally extended, or but slightly inclined. The other leaf-stalk, however, rises vertically from the horizontal twig; the leaf-blade it supports is bent down at right angles from it, and consequently is here again parallel to the surface of the ground. A slight torsion of the internodes, a shortening of the erect leaf-stalks, and a diminution of the leaves

borne by them, certainly assist in the completion of this peculiar arrangement of the leaves; the above illustration will demonstrate other particulars far better than the most detailed description.

The elevation of individual leaf-stalks above the horizontal branches occurs, somewhat more often in low semi-shrubs and herbs, than in trees and shrubs, whose shoots, furnished with decussate leaves, come to lie flat on the ground, as in some species of speedwell (*Veronica officinalis* and *Chamædrys*), and in many species of Rock Rose (*Helianthemum*). In the large-flowered Rock Rose (*Helianthemum grandiflorum*), an erect branch of which is illustrated in fig. 107 [1],

Fig. 109.—Leafy Twig projecting laterally from the Stem of the Norway Maple (*Acer platanoides*).

the leaves are arranged in pairs and placed crosswise, so that they occur on the stem in four rows. If such a shoot bends down over the ground, a slight twisting of the leaf-stalks occurs first of all, so that their leaf-blades come to lie parallel to the soil; but another alteration is yet to be noticed. In every alternate pair of leaves one of the leaf-stalks rises up, and its blade is bent down almost at a right angle and lies above the horizontal stem as shown in fig. 107 [2]. In consequence of this alteration of position the leaves no longer form four rows as on the erect shoots, nor two as in *Diervilla*, but three rows, the middle one, however, consisting of a smaller number than the two side rows.

The fourth case, which still remains to be discussed, is the increase in length of individual leaf-stalks. It may be very well seen in maple-trees, especially in the Norway Maple (*Acer platanoides*), and this species will therefore serve us as an example. Fig. 106 shows an erect branch of this maple. The stalks of every pair of opposite leaves are of equal length on the erect branch. But how entirely different in respect to length are those leaf-stalks which embellish the horizontally-

directed branches of this species. Here one of the pair always appears considerably longer than the other; and it is not a rare occurrence for it to be three times as long as its neighbour, as may be seen in figure 109. And why this striking dissimilarity? The reason is again the same as in all the previous cases. If all the leaf-stalks were to retain the same length on the horizontal twigs which they have on the erect branches (see fig. 106), then one of the leaves of every alternate pair would come to be very unfavourably situated in its neighbour's shadow. This detrimental condition must be prevented, and this may be effected most simply by the leaf-stalk increasing in length until the blade it carries is projected beyond the area of the shadow.

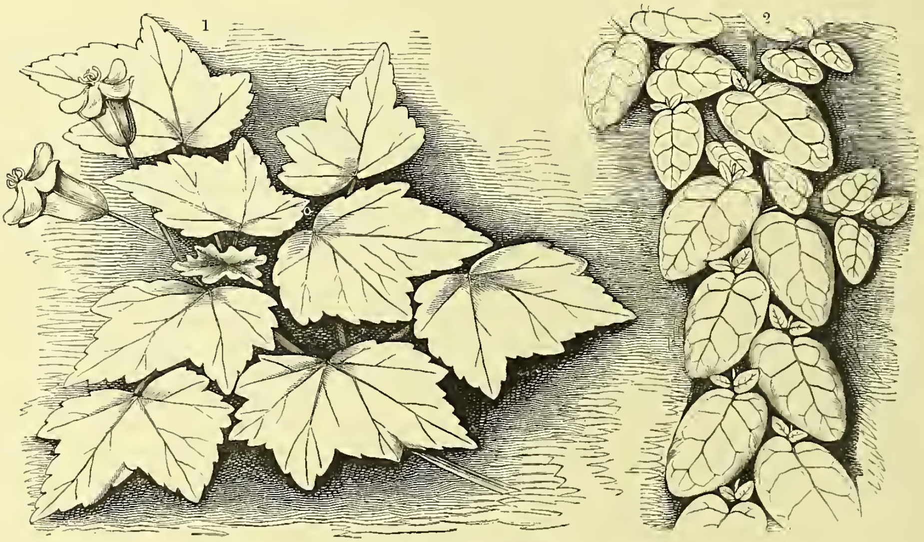


Fig. 110.—Leaf-mosaics of Unsymmetrical Leaves.

1 *Begonia Dregei* growing in front of a vertical wall. 2 *Ficus scandens*, growing on a vertical wall.

It may be expected that alterations of direction, shortenings and elongations, similar to those just described in the case of the horizontal leafy twigs of the lower boughs of trees, shrubs, and bushes, will be found on those plants which are attached to a steep face of rock, a vertical wall, or to the bark of an upright tree-trunk. As a matter of fact all the instances discussed here are again met with in various climbing and twining growths, as well as in those whose stem is parallel to a vertical wall without being attached to it, *e.g.* as in *Rhamnus pumila*, and in many begonias. But here the leaf-blades do not place themselves parallel to the ground, but to that surface on which the plants in question are supported, or which they adjoin. In these plants another peculiarity is often observed which it will be most fitting to speak of here, viz. the want of symmetry of the leaves. While in the majority of plants each foliage-leaf is divided by a midrib, running from the apex to the leaf-stalk, into two similar or almost similar halves, in the begonias, many climbing figs, in *Celtis occidentalis*, elms, and numerous other plants, the two

portions of the leaf separated by the midrib are very unlike. The dissimilarity is seen principally at the base of the leaf—it looks as if a piece had been taken out of one side, or as if the leaf had there been cut off obliquely (see fig. 110). The correct explanation of this want of symmetry will perhaps be arrived at most easily by supposing the suppressed portion to be completed, or in other words, let us suppose the smaller half to be just as large and well-developed as the other. It is then evident that the added portions would be covered over by the neighbouring leaves, and consequently they would be deprived of light, and that in these parts, therefore, the chlorophyll-bodies, if present, would not be able to

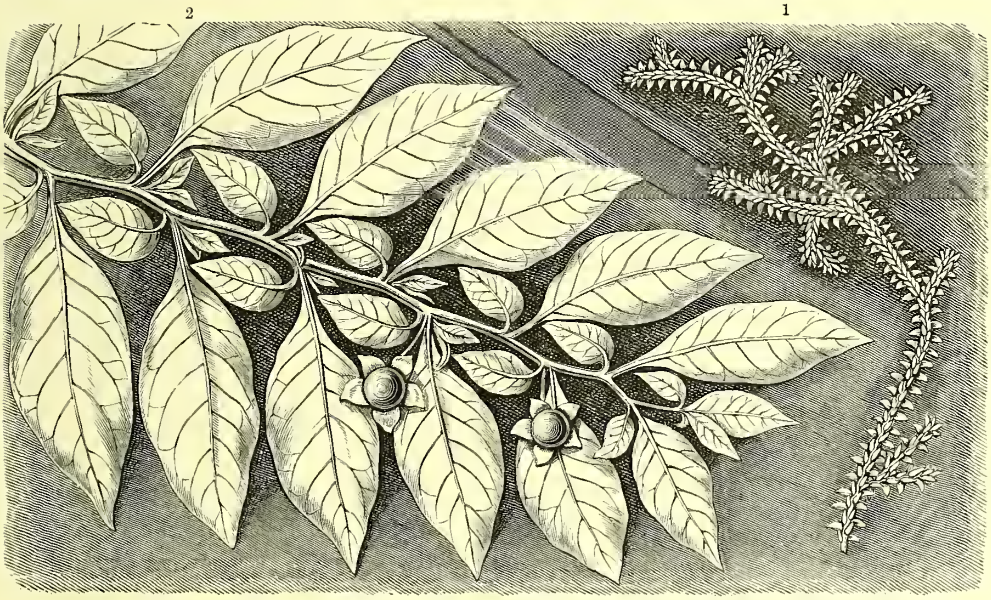


Fig. 111.—Mosaic of Leaves of unequal size.

1 Projecting branch of Deadly Nightshade (*Atropa Belladonna*) looked at from above. 2 *Selaginella Helvetica*, seen from above.

carry on their activity. These portions of the foliage-leaves would accordingly be superfluous, and it is foreign to the ways of plants to manufacture so much leaf-tissue for no purpose whatever. Plants never form anything which is superfluous and useless; in the construction of all the organs the principle apparently is to attain the greatest possible result with the least amount of material, and to utilize the given conditions, above all, the existing space, as far as possible.

Yet another phenomenon, viz. the unequal size of adjoining leaves on the same plant, must be considered from this point of view. It must strike everyone who looks down upon a horizontally-projecting branch of the Deadly Nightshade (*Atropa Belladonna*, see fig. 111 [1]), that larger and smaller leaves are here arranged in quite a peculiar manner. The larger leaves stand in two rows, and in virtue of their shape it happens that, between every two, gaps are left near the stem.

These cannot be of use as apertures, through which light can pass to leaves situated below, for the simple reason that, as a rule, no other leaves requiring light are to be found under the branches in question. Smaller green leaves are now inserted in these gaps, which serve as protective leaves for the flowers, that is, indirectly for the fruits, but whose function also coincides entirely with that of the large foliage-leaves. The small leaves twist and turn until each comes to lie exactly in the middle of a gap, where they neither encroach upon the large leaves, nor are encroached upon by them. An exactly similar insertion of smaller leaves in the gaps between the larger can also be observed in the Thorn-apple (*Datura*

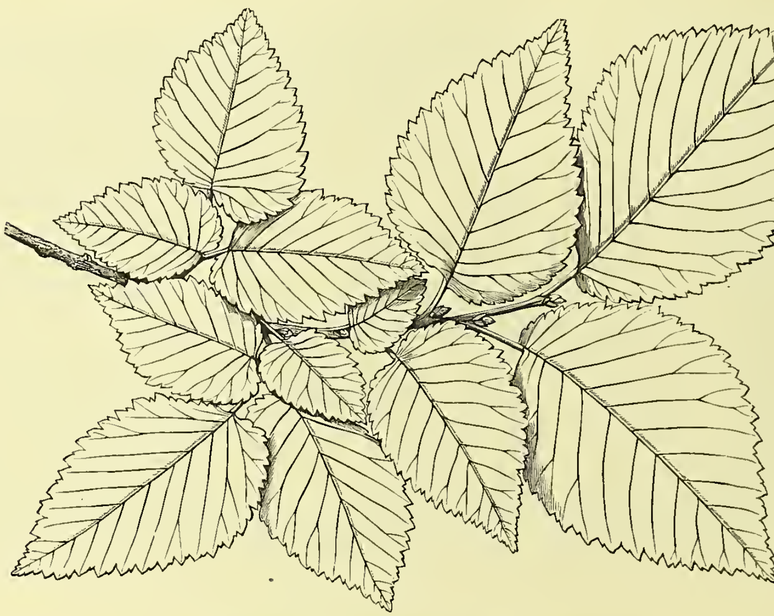


Fig. 112.—Mosaic of Unsymmetrical Leaves of unequal size.

Leafy horizontal Twig of an Elm (*Ulmus*) seen from above.

Stramonium), and in *Impatiens parviflora*, illustrated respectively in fig. 104 [3], and fig. 104 [1]. This mosaic-like fitting together of larger and smaller blades appears to be combined with the want of symmetry of the leaf-base in short-stalked leaves, as *e.g.* in the wall-climbing stem of *Ficus scandens* (see fig. 110 [2]), and on the older horizontal branches of elms (*Ulmus*), one of which is illustrated in fig. 112. It has been already mentioned that the blades with erect petioles, arranged in the central rows on the Paper Mulberry, are considerably smaller than the lateral rows of leaves with horizontal stalks (see fig. 108). This difference in the size of the central and lateral rows of leaves on horizontal stems is very noticeable also in the dainty selaginellas, belonging to the family of Lycopodiaceæ, of which a species (*Selaginella Helvetica*) is represented in fig. 111 [2].

It is worth noticing that the occurrence of leaves of two sizes on the same stem, as well as the mosaic-like arrangement and fitting together of the leaves in one

plane, is observed especially in plants growing in dark or half-shaded places. There they do not require to protect themselves against an over-abundance of light, but on the contrary have to make what use they can of its scanty amount, and this is best effected by the fitting together of all the leaves on a stem in one plane, like the stones of a mosaic. It is, of course, not so easy to produce a mosaic from symmetrically circular or elliptical leaves; but unsymmetrical, or rhomboidal, triangular, pentagonal, and, generally, polygonal blades lend themselves particularly well to this arrangement. Excellent examples of this are furnished in the leaf-mosaics in fig. 110, as well as in the elm twig represented opposite. The leaf-mosaic formed by the ivy on the ground of shady woods is particularly instructive in this respect. In the picture below, which is a faithful reproduction of a piece of ivy carpeting the ground of a wood, it is seen how the lobed, five-pointed leaves

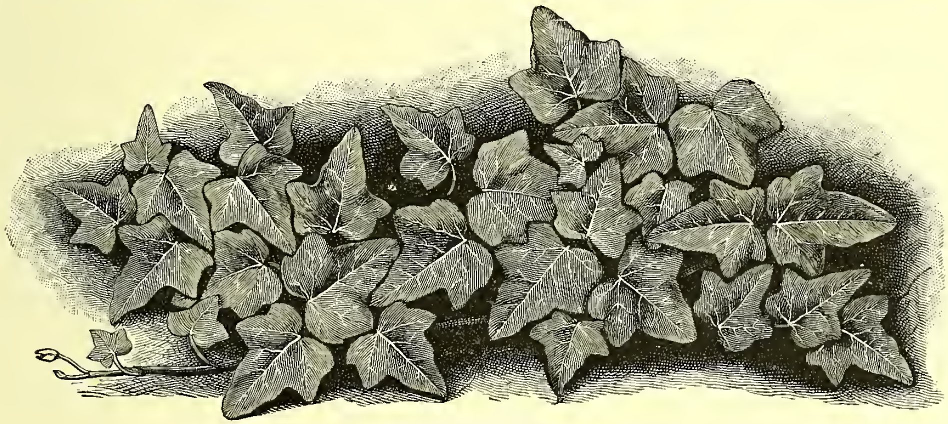


Fig. 113.—Leaf-mosaic.
Ivy on the ground of a forest.

have in the course of time fitted into one another. The lobes and points of one fit into the indentations of another, and thus originates a layer of leaves than which one better fitted to the given external conditions could hardly be imagined. In this mosaic, indeed, we no longer see two rows of leaves symmetrically arranged on the horizontal stem. What manifold elevations and depressions, torsions, displacements, and elongations must have taken place in order to produce such a leaf-mosaic from the regular rows of leaves! But we learn from the consideration of all these instances, that not only the arrangement and distribution of the foliage, and the direction and length of the leaf-stalks, but the size and even the shape of the leaf-blades also, and the resultant mosaic-like piecing together, stand in causal relation to the conditions of illumination; and that in dimly-lighted situations plants endeavour to utilize, and turn to account, the sunlight for the green tissue of the foliage-leaves as far as possible by the means at their disposal, and with regard to the given conditions of space.

ARRANGEMENTS FOR RETAINING THE POSITION ASSUMED.

When the green tissues of plants have once assumed the position most beneficial to them, they must be kept as long as they can be in that position, and any further alteration must be as far as possible avoided. The displacements, curvatures, and extensions described in the preceding pages, representing a struggle for the best arrangement of the green tissue for light, must not be restricted; whilst distortion, folding, and rupturing of the chlorophyll-containing tissues, which would be synonymous with the destruction of the portion in question, must obviously be warded off.

In the depths of still water, at the bottom of pools, ponds, and lakes, an alteration of the position assumed by the fully-developed plants in consequence of an external stimulus occurs but seldom; and although currents and eddies are set up in the water by passing aquatic animals, and temporary oscillations caused in the water-plants, these quickly subside, and the agitated portions return forthwith to their original position, having suffered no injury. In aquatic plants of this kind there are no special contrivances for strengthening the individual organs, and in particular no contrivances for protecting the green tissue from rupture and crushing. The small amount of strength and elasticity of the cell-walls suffices to withstand the thrusts, and pulls, and the pressures which make themselves felt in the depths of the water, and to restore the temporarily displaced green portions to their right position. Firm woody cells, and strands of elastic bast-fibres, which play such an important part in the aërial portions of plants, are wanting here. Woody plants neither grow in the sea, nor in fresh water. Aquatic plants, indeed, quickly collapse, in consequence of the absence of wood and bast, when brought from the depths into the air; the leaves collapse of their own weight, and sink flaccidly on to the substratum. They are able to retain an erect position in the water, because a portion of their tissue is penetrated by comparatively large air spaces, by which means their specific gravity, compared with that of the water, becomes much diminished. If aquatic plants were not firmly attached to the sand and slime, or submerged rocks, they would rise to the surface and float there. But as they are fixed in the depths, the air spaces within the green tissue of the leaves or stalks bearing the leaves cause these organs to remain erect as if suspended in the water.

Plants growing in running water, and such as are exposed to the lapping of the waves on the shore, are indeed subjected to a severer proof of their firmness and tenacity. Thus many of them, *e.g.* sea-wracks on the sea-coast, the long-leaved pondweeds in the quick-flowing mountain streams, and the Podostemaceæ in the rushing torrents and waterfalls in tropical regions, are actually swayed hither and thither and continually shaken, and accordingly due allowance must be made in their construction for this circumstance of their habitat. The tissue of these plants is much tougher than that of the Characeæ, of the Naiadaceæ,

of Water Milfoil, and of various others which lead a peaceful life in the depths of calm waters. Their tissues are not feeble, but elastic and pliant, and many sea-wracks look just like leathern straps and bands. Many of these sea-wracks are periodically left lying on the dry ground at low tide, but they do not in consequence shrivel, or at least not if the water soon returns, but lie with their pliant leaf-like surfaces flat on the dry sand or stone. When the tide returns, they are again gradually raised up, and assume an upright position in the surrounding water; and this is materially assisted in the sea-wracks by the swollen bladder-like cavities, in reality swim-bladders, which they contain in their tissues. Many species of Characeæ, but still more the Lithothamneæ and Corallineæ, acquire an increased capacity of resistance against the force of the waves by the deposition of lime in the cell-membranes; others again so closely apply their large surfaces to the rocky reefs and stones of the shore, that they look like coloured patches on them, so that the crushing or tossing effect of the surging waves is entirely obviated. This applies, for example, to *Hildebrandtia rosea* and *Hildebrandtia Nardi*, which cover the stones with blood-red patches.

Many marsh-plants, which are only partially, and often only temporarily, submerged, whose floating leaves are half in contact with water and half with air, or whose leaf-blades are wholly raised above the water, behave just like these water-plants. The alteration of the water-level brings about, of course, a higher or lower position, on elevation and sinking of the floating leaves, but this is effected without the slightest rupture of the parts in question. The stem and the leaf-stalks, which proceed from a stock rooted at the bottom of the water, resemble long strings and threads to whose upper ends the leaf-blades are fastened. At the highest water-level the floating leaf-discs stand perpendicularly above the stock to which they belong, which is rooted in the depths. If the water then sinks, the leaves, floating on its surface, fall with it, and at the same time separate from one another. The stalks and stem proceeding from a stock perform approximately the same movement as that seen in the ribs of an umbrella held downwards and then opened. As soon as the level of the water rises again, the reverse movement naturally occurs. Many of these marsh-plants, as, for example, the Water Chestnut (*Trapa*), also possess air-bladders in the floating portions of their leaves, having the same function as those of the sea-wracks. Moreover, usually two kinds of green foliage-leaves are noticed in these. Submerged leaves, which are constructed like those of aquatic plants, and floating leaves which display a more or less disc-like form, and whose under side is in contact with the water, the upper with the air, but which under certain circumstances may be entirely surrounded with air without injury. If the marsh should dry up, long thin stems and leaf-stalks would be anything but beneficial; the metre-long leaf-stalks of a water-lily would not be able to support the leaves in an erect position, but would fall and become bent. Stretched out on the ground, also, such long filamentous leaf-stalks would not be advantageous. It is seen, too, that marsh-plants of this kind immediately become modified when the water recedes. The

fresh leaves have only short stalks, and these become so strong and elastic that they are well able to support the leaves. Water-lilies are striking examples of this. In *Polygonum amphibium*, the long stems of the aquatic form, bearing at their upper ends groups of floating leaves, are much thinner than the short stems of the terrestrial forms, which are uniformly beset with leaves from top to bottom.

The green tissues which are surrounded with air are much more exposed to the danger of being torn, bent, and broken up by violent gusts of wind than those which live either wholly or partially submerged in water.

When green tissue is only developed in the cortex of the branches, as in the leafless switch-plants, the branches are always elastic and supple, and in order to produce this quality, bundles and strands of hard bast, *i.e.* elongated spindle-shaped thick-walled cells of fibrous appearance, are inserted at suitable places. The wood in these branches is also very tough, and gusts of wind can consequently do them little harm. They are often prostrated by storms; but when the wind subsides, the branches forthwith rise up, and in consequence of their elasticity, resume their former position towards the light. The bundles of hard bast-cells alternate in many instances regularly with the green tissue, as, for example, in *Spartium scoparium*, illustrated in fig. 81, and, generally, very manifold contrivances are to be found in the internal construction of the branches for hindering the bending up and crushing of the green tissue.

Leaves, as well as stems and branches, have originally a tendency to grow up perpendicularly in the atmosphere, and there are many plants whose foliage remains throughout life in this position. Obviously these leaves are no less exposed to damage by storms than are the upright branches of the switch-plants. It must be borne in mind that gusts of wind rush over the ground in waves like a powerful torrent, and that the direction of the air-current is usually parallel to the surface of the earth. Plant-organs which grow up from the ground are struck at right angles by such gusts, and are thus exposed to the most violent attacks of the wind. Leaves, especially, whose blades are inclined at right angles to the direction of the storm, are much more easily bent and crushed than those whose blades lie parallel to the current. The effect of the attacks of wind increases in proportion to the extent of the surface exposed to the air-current, and a large upright projecting leaf will be bent much more by the wind than a small leaflet which lies close to the stem like a scale.

In what way can the dangers of rupture be warded off from a green leaf which grows towards the light of heaven, is surrounded by air, and is exposed on all sides to the attack of wind? First of all, at any rate, by the same developments as those mentioned in the case of the upright green branches of switch plants, *i.e.* a suitable placing of the green tissue between flexible, elastic, fibrous bundles of bast-cells, by support from thick-walled woody cells, and other cellular formations; by these means firmness is given to the whole structure with the least possible expenditure of material; an arrangement which the thin-walled green tissue can, by itself, never have on account of its special function.

But the whole shape and position of the leaf must also be adapted to the circumstances, for the simple reason that a plant constructed unsuitably with regard to the prevalent winds would suffer injury, perish, and sooner or later be supplanted by other species better adapted to the given conditions. Therefore, it may so far be looked upon as an adaptation of form when a leaf lies with its surface parallel or only slightly inclined to the surface of the earth, and therefore to the direction of the wind, so that the moving currents strike it at a very oblique angle, and rupture of the blade can hardly ensue. Since this position of the green leaves is also very favourable for most plants with regard to light, it is not surprising that it occurs so generally. In such flat leaves, a rising and falling, and occasionally a bending of the blade is unavoidable, especially when the gust of wind comes from that side towards which the tip of the leaf is turned. But such an attack on the leaf-blade, which is parallel to the surface of the ground, or inclined slightly to the horizon, is rendered as little injurious as possible by two arrangements.

One consists in the fact that the moderately stiff leaf-blades can turn like weathercocks on the stem from which they project; this occurs in many reed-like grasses, particularly in *Phalaris arundinacea*, *Eulalia Japonica*, and in the widely-distributed *Phragmites communis*. The latter, which often grows in immense quantity in the marshy lowlands, in the depth of valleys, and on the banks of rivers, develops lofty, slender culms bearing numerous leaves. These leaves, like all grass-leaves, consist of a linear, fairly broad, and tapering blade projecting from the stem; and also of a sheath in the form of a hollow cylinder surrounding the haulm, and from which the portion of the haulm in question proceeds as from a tube. As long as the haulms and leaves are not fully developed, the leaf-blades are strongly directed in a line parallel to the culm; later, they decline, project horizontally, and finally become even somewhat depressed, so that their apices are directed groundwards. They then remain flat, and are so stiff that they cannot be bent by light winds. Moreover, if a stronger gust occurs, they do not bend, but twist round like the weathercock on the roof-gable in the direction of the wind. This is rendered possible only by the fact that the haulm and the tubular leaf-sheath surrounding it are very smooth at the surfaces in contact with each other, and that the leaf-sheath may undergo a slight splitting without damage.

This development is found in the reed-like grasses mentioned; and in them there is a further contrivance, an interrupted membrane or flap inserted at the boundary between the blade and sheath; this protects the sheath from the entrance of rain-water, and consequent increase of friction, rendering the twisting difficult. The common Reed (*Phragmites communis*), growing in quantities, presents a characteristic appearance, in consequence of the arrangement here described, every time a breeze passes over such a bed. If the wind blows from the east, all the leaves are directed to the west; if it comes from the west, all their apices are turned to the east. The whole mass looks as if it had been combed, as if all the

leafy blades had been stroked like the hair of a horse's mane in the direction of the wind.

The second arrangement for protecting broad flat leaves against crushing is observed in fan-palms, in maples, poplars, birches, in pear and apple trees, and in innumerable other woody growths of all regions. It consists in the development of long, elastic leaf-stalks. The Aspen (*Populus tremula*), which may be regarded as the best example, exhibits leaves on the branches of its crown, whose circular blades are always somewhat shorter than the stalks. At the slightest movement of the air these are seen to tremble and sway hither and thither, and this phenomenon is so striking that it has furnished the nucleus of many sayings, such as to "tremble like an Aspen leaf". But even in the most severe storms it is only the leaf-stalks which bend, having acquired a high degree of elasticity by the development of bast strands. The leaf-blades borne by them remain flatly extended, stiff, and rigid. They are not bent by the wind, and, therefore, these elastic leaf-stalks ward off the danger of fracture from the blades they support.

In many grasses—for example, in the most widely-distributed cereals, wheat, rye, and barley—it is observed that the first green leaves developed by the seedlings are erect, while those developed later, which arise from the slender haulm which springs from their midst, are more or less parallel with the ground. In many other plants with much contracted subterranean stem-structures, viz. in the Reed-mace (*Typha*) and in many bulbous plants, all the foliage-leaves assume an erect position and remain so until they fade and die. Leaves, when erect, are far more exposed to the wind passing horizontally over the ground, and require much stronger protections against bending than those which are extended flatly over the soil; and in order that they may be able to escape fracture, they must be provided with specially effective contrivances.

The *fistular* leaf is to be regarded as one of the most striking of these contrivances. Fistular leaves are always erect at the lower end, where they surround the stem or the neighbouring leaves, like the equitant leaves of irises; they are sheathing and hollow, terminating above in a hollow cone. There is no conspicuous midrib; a shallow groove is frequently seen on the side directed towards the central axis of the whole plant; otherwise the hollow leaf is developed uniformly all round. It has no appearance of special resisting capacity, and those cellular elements which, as a rule, are used to increase strength, are absent; and yet, like all tubes, it possesses a relatively great resistance to flexion, and it is scarcely injured, even in violent storms. On the whole, this striking form of leaf is not common; it is most often seen in bulbous plants, *e.g.* in Chives and in the Common and Winter Onions (*Allium Schœnoprasum*, *Cepa*, and *fistulosum*). Structures are more often met with which resemble the fistular form to some extent, since their long green blades are rolled up lengthwise, sometimes towards the side facing the central axis of the whole plant, and sometimes away from it. The rolling observed in leaves of crocuses is particularly noticeable. A white central strip runs the whole length of the erect leaf, which is bordered by two

green bands. At first sight these two green bands appear to be flat, but they are not really so; each is convolute, and thus in the crocus-leaf there are actually two green tubes united to the white central stripe, which is destitute of chlorophyll. This leaf may be distinguished by its erect position from the rolled leaves which have been described in detail, and which are similar in some respects, although they differ from them in significance.

The *spiral* leaf furnishes another contrivance of this kind. It is frequently seen in the leaves of bulbous plants, bur-reeds, and grasses, principally in young plants—as, for example, the first green leaves of barley and rye. Leaves spirally twisted like this are always long, narrow, and erect. Sometimes but a single spiral revolution is found, or even only a half revolution; sometimes two, three, often even four circuits are described. The leaves of the New Zealand Flax (*Phormium tenax*), and those of the Asphodel (*Asphodelus albus*), of narcissus, of many irises, and of some pines, exhibit only a half, or at most only a single spiral twist; those of the Lesser Bulrush (*Typha angustifolia*), and numerous species of Garlic (*Allium senescens, rotundum, obliquum*) present two to three, those of *Sternbergia Clusiana* three to four, and the Persian *Sternbergia stipitata* five to six revolutions. Leaves of this kind have, consequently, a curled appearance. That such a spiral leaf resembles the fistular leaves in its mechanical significance, and that it possesses a greater resistance to flexion than a flat leaf, is beyond question.

It may also be noticed in the Reed-mace, that in a strong wind the leaves are not only bent, but are also somewhat elongated, *i.e.* the spiral becomes somewhat looser in the bent leaf. But as soon as the wind subsides, and the leaf returns to its vertical position, the previous form of torsion is resumed. The advantage possessed by an upright spirally-twisted leaf over an erect flat one, with regard to wind, becomes quite obvious when one imagines the two forms exposed side by side to the same wind-pressure. When the gust strikes an erect flat and rigid leaf, the whole of its surface is encountered at right angles, and the leaf undergoes a large amount of bending, and possibly fracture; but when it strikes a spirally-twisted erect leaf, the various portions of the blade are met at different angles; the air current becomes, as it were, diffused into innumerable streams, which, passing along the revolutions of the spiral, effect only a comparatively small curvature, and scarcely ever cause the leaf to be broken. When these spiral leaves are swayed by the wind, from a distance the movement has a very peculiar look, much more like trembling, tossing, and twisting than like bending.

The arched form of leaf is closely allied to the spiral. It, too, is found in long ribbon-shaped leaves. At the commencement of development the arched leaf is erect and lies in one plane, but when fully developed it takes the form of a bow, with the convex side directed upwards. It may spring from the sides of erect lofty stems, or may originate close to the soil. Arched leaves appear very noticeably in those grasses whose habitat is on the ground in, and at the margins of, woods and on steep mountain slopes, *e.g.* in *Milium effusum, Melica altissima, Calamagrostis Halleriana, Brachypodium silvaticum, Avena flavescens,* and

Triticum caninum. When the wind sways the leaves of these plants, the arch formed by them is either narrowed or widened, according as the wind comes from this or that side. In still air the leaf assumes a middle position. Although the arch may be widened or narrowed by the wind, in no case does the bending go so far as to break the blade. Moreover, these leaves are rendered so elastic by a suitable arrangement of bundles of bast, that even violent storms cannot do them much harm. These arched, overhanging, ribbon-like leaves are often further complicated by the fact that all the leaves are turned to the same side so that they present a combed appearance—like those of the reed—although their sheaths cannot twist round the haulm. This is seen especially when the plants are growing on the margin of a wood or on the narrow terraces of a rock face, *i.e.* on places where they are only illumined on one side. The one-sided direction of the leaves is connected with the illumination, and is due to the fact that a semi-arched leaf turned towards the gloom of a wood, or towards a shady rock-wall, would not obtain sufficient light. This gives rise, indeed, to an inversion of the leaf-blade, so that the originally lower side of the leaf becomes the upper.

It is scarcely necessary to state that the relations with regard to light exercise a no less important influence in the determination of the shape of the spiral and fistular leaves than in the above-mentioned grasses, whose leaves are arched, overhanging, and partially twisted. If these relations are not taken into consideration, it is not because the significance of light in these special instances is not appreciated, but only because a clear view of these extremely complicated conditions can only be obtained by a rather one-sided treatment.

PROTECTIVE ARRANGEMENTS OF GREEN LEAVES AGAINST THE ATTACKS OF ANIMALS.

The matrix of the chlorophyll-granules is very similar in composition to that of protoplasm, and, like it, consists of nitrogenous compounds; by the activity of the chlorophyll-bearing cells sugar and starch are produced, and the green cells contain not only albuminous compounds, but also carbohydrates, and these, too, in a form in which they are digested with comparative ease. What wonder, then, that these green cells furnish a very desirable food for innumerable animals. Many animals, it is well-known, live exclusively on a vegetable diet, and principally on chlorophyll-bearing tissues. On the other hand, the plants in question would perish with the loss of all their green organs, especially if the store of reserve food in them were also exhausted. The animal and vegetable kingdoms in this sense are at war with one another. The instinct of self-preservation forces animals living on green vegetables to seek their food at any cost, to seize the plants unsparingly, and when their hunger presses, to destroy them root and branch. Herbivorous animals cannot, like men, foresee that in the consumption of the means of subsistence the plants robbed of all their green organs must perish, that consequently in the following years for them and their descendants food will be wanting, and that

in the destruction of their food-plants, their own existence is imperilled. If man removes a portion from the plants serving for his livelihood, a limit is always fixed to this consumption which prudent consideration and foresight never overstep. He always leaves as much as is necessary to the plant in order that it may maintain itself and multiply. Indeed, he even tries to assist and to further the nourishment, growth, and multiplication of the plants useful to him, and is at considerable trouble to protect and to save serviceable vegetation from the ravages of animals. This protection of man, however, is limited to a comparatively small section of plant species; all those from which he derives no benefit remain uncared for, and these would be surrendered to the overwhelming onslaughts of animals, and final destruction, if means were not at their disposal by which they could protect and maintain themselves. Of course these means are not adapted to offensive attacks upon the animal kingdom; and the attitude of the vegetable world towards animals must not be looked upon as one of war, but rather as an armed peace.

But if plants have only at their disposal means of defence, these are none the less dangerous to offenders, and not only equipments comparable to pointed weapons, but also poisons and corrosive fluids are abundantly turned to account.

First of all, with regard to *poisons*. It is to be pointed out that these are only developed in those parts and to an extent necessary in order to preserve at least the greater portion of the foliage, and then also the flowers and fruit. Moreover, it must be remembered that the same chemical compound does not act as a poison to an equal degree in all animals. The foliage of the Deadly Nightshade (*Atropa Belladonna*) is a poison to the larger grazing animals, and by them is left undisturbed; but the leaves of this plant are not only non-poisonous to a small beetle (*Haltica Atropæ*), but form this animal's most important food. The larvæ of this beetle often eat numerous holes in the leaves, which, however, by no means prevent the development of the Deadly Nightshade. Accordingly these leaves are protected by the alkaloid contained in them only against wholesale extermination; limited portions of them can be surrendered and sacrificed with impunity. The same thing occurs in numerous other plants which contain poisonous alkaloids, or other materials harmful to large herbivorous animals. It is puzzling how grazing animals find out the materials in the leaf which are injurious to them. In many instances the plants in question possess characteristic odours which act offensively on the olfactory nerves of men at any rate, as, for example, the Thorn-apple (*Datura Stramonium*), the common Henbane (*Hyoscyamus niger*), the Hemlock (*Conium maculatum*), the common Birthwort (*Aristolochia Clematitis*), the Dwarf Elder (*Sambucus Ebulus*), and the Sabin (*Juniperus Sabina*); many other poisonous species, however, which are likewise avoided by grazing animals, bear leaves which to men are odourless as long as they are intact—as, for example, the numerous species of Monkshood (*Aconitum*), Black Hellebore (*Helleborus niger*), the White Hellebore (*Veratrum album*), the Meadow Saffron (*Colchicum autumnale*), the Mezereon (*Daphne Mezereum*), species of Spurge (*Euphorbia*) and Gentians (*Gentiana*), which are never disturbed by stags, roes, chamois, hares, and just as

little by oxen, horses, and sheep, not even by the omnivorous goat. As long as the plants remain undisturbed in wood and meadow, their characteristic materials have no effect on the olfactory nerves of men, but they must make themselves known to the animals mentioned by the sense of smell, and this even before the plants have been bitten and injured. The fact that plants which contain no alkaloids, and generally are not poisonous to men, are at the same time carefully avoided by grazing animals makes it probable that to eat them would be in some way injurious to these animals. This remark applies particularly to mosses, ferns, succulent plants (*Sempervivum* and *Sedum*), many cresses (*Lepidium Draba, perfoliatum, crassifolium*), Toadflax (*Linaria vulgaris*), the Greater Plantain (*Plantago major*), and many oraches.

That horse-tails (*Equisetum*), the green leaves of the Crowberry and Bearberry (*Empetrum* and *Arctostaphylos*), the Rhododendron and Cowberry (*Rhododendron* and *Vaccinium Vitis-Idæa*), and numerous other low evergreen shrubs, which form a chief constituent of the vegetation of heaths and moors, as well as the declivities of high mountains; further, that the Proteaceæ and Epacrideæ which compose the bush of Australia and the Cape, are avoided by the animals seeking their food there, is indeed explained by the fact that the tissue of these plants is very difficult to digest in consequence of strongly developed and partially silicified cuticular strata. It is certain, therefore, that in the formation of a very thick, firm cuticle, and in the deposition of silica in the cell-wall, a protective measure is provided against the attacks of grazing animals; though, of course, it must not be supposed that this is the only function discharged by these structures.

In many plants *water* forms an excellent protection against grazing animals, including that which falls as rain and dew on the foliage-leaves, and then remains for days and even weeks collected in special hollows. In the morning when the plants are richly bedewed, the ruminants do not usually graze; they wait until the cold dewdrops and rain-drops which adhere to the leaves are evaporated; and later also, they leave on one side those plants on which the rain-drops still remain. In this respect the Lady's-mantle (*Alchemilla vulgaris*), known also in popular language by the name of Dew-cup (illustrated in fig. 52 [2]), is a very striking instance. Rain and dew remain collected here at the bottom of the cup-shaped leaves, when already, in the meadow round about, the surfaces of other plants have become quite dry. While these latter, if they are not protected in other ways, are devoured by the grazing animals, the Dew-cups remain undisturbed, and are evidently avoided. This is not caused, as in the ferns, by the possession of certain objectionable materials—since the leaves of an *Alchemilla*, from which the water has been shaken, are eagerly taken as food by the grazing animals, which must, therefore, in some way dislike to feed on leaves on which water is standing.

The most important rôle in the defence against food-seeking animals is performed by the organs terminating in strong, tapering, sharp points, which wound offenders, and may be called the weapons of plants. In botanical

terminology they are known as *spines* and *prickles.* A structure which is mainly composed of wood, or whose interior is at least traversed by vascular bundles springing from the wood, and which, therefore, ends in a firm sharp point, is called a spine (*spina*). On the other hand, a prickle (*aculeus*) is a structure which proceeds from the epidermis or cortex of a plant member, contains no vascular bundle within, may be multi- or unicellular, but always terminates in a point which is capable of wounding the skin of the offender. This distinction is not always an easy one to make, and botanists have never laid much stress upon it.

Spines and prickles may arise from all the plant members and organs, and appear at all heights. They are observed most usually on or near the green tissues to be protected, but often even the road to the green organs, passing over the leaf-stalk, the stem, and occasionally also over aërial roots, is provided with prickles and spines in order that in this way the animals which feed on vegetables, particularly snails, which creep up from below, may be kept off. Thus very pronounced spines are seen, for example, on the aërial roots springing from the lower part of the stem in *Thrithrinax aculeata.* The lower portions of the main axes up which these animals must climb in order to reach the green portions are armed with spines or prickles, in many *Bombax* and *Pandanus,* in Erythryneæ, gleditschias and roses, and in the fan-palms very abundantly on the leaf-stalks.

The size, direction, position, and distribution of the weapons depends generally upon the nature of the attack, on the form and size of the food-seeking animals, and on the nature of the implements at their disposal. The gigantic floating leaves of the *Victoria regia* are only armed with prickles on the under surface and on the turned-up margin, *i.e.* only where they are exposed to the attacks of plant-eating aquatic animals. It is also an interesting fact that many woody plants are only protected when young, *i.e.* while they are short and their foliage can be reached by ruminants, viz. by goats, sheep, and oxen; but on the boughs and branches removed beyond the reach of the mouths of these animals, no prickles and spines are developed. Young, low trees of the Wild Pear, only one or two metres in height, bristle with the spines into which the ends of the woody branches are transformed; while the branches of the crown of trees four or five metres high remain without spines. The same thing occurs in the Chinese Gleditschia (*Gleditschia Chinensis*), and in the Holly (*Ilex Aquifolium*). In the latter it can be seen that the leaves of the crown of tall trees have almost entire margins and are unarmed, while the margin of the leaves in shrubby specimens is drawn out into bristle-like, pointed teeth.

Plants armed with weapons for warding off the attacks of animals may be arranged together in two groups. One of these consists of those forms which protect their green tissue by structures actually developed on the organs in question, and the other group comprises those forms which have no such capacity of self-help, where, rather, one member protects another, and where division of labour has brought it about that certain plant-organs deprived of chlorophyll

and metamorphosed into weapons assume the protection of the unarmed adjoining chlorophyll-bearing members.

To the first division belong chiefly most of those leafless plants which have developed green tissue in the cortex of their branches and twigs. Indeed, the green branches of these plants are, as a rule, so firm and rigid that one would imagine they would scarcely ever tempt animals to eat them. But "hunger is a hard master", and in cases of necessity, as shown by experience, even the stiff switch-like shrubs of the Mediterranean and other floral districts are attacked. In order that they may not succumb entirely to these assaults, many of the leafless green-branched plants are suitably armed by the possession of spines at the ends of their green branches, which confront the assailants. Many of these plants, indeed, are actually built up entirely of much-branched green spines, which fact, of course, gives them a very peculiar appearance. The spinose flora of Spain and of the opposite coast of Africa exhibits a whole series of these plants, but here only the Furze (*Ulex nanus, Gallii, micranthus*), and the spring Asparagus (*Asparagus horridus, Broussonetia,* and *retrofractus*) need be cited as examples. Also the green leaf-like branches of plants with flattened shoots, which are not protected by poisonous substances like those of *Phyllanthus,* run out into sharp points, as may be seen in the European Butcher's-broom (*Ruscus aculeatus*), illustrated in fig. 82, and in the South American *Colletia cruciata,* represented in fig. 83 [1].

The weapons developed on green leaves are far more complicated than the implements with which green stems are furnished. In some instances points which wound aggressors project from the ends of the ribs and veins which form the groundwork of the leaves, rising up like needles above the green tissue of the foliage; in other cases they consist of cells and groups of cells which originate from the epidermis of the green leaf, and are inserted, sometimes at the margin, sometimes on the surface, like little daggers. In the first instance the vascular bundles, which are seen traversing the leaf as ribs, are provided, at the point where they project beyond the green tissue and terminate as spines, with a covering of very hard cells; in the latter case the cells and cell-groups springing from the epidermis and rising up as prickles, bristles, and pointed hairs, exhibit thickened and strongly-silicified walls. The following equipment appears particularly often in several pines, many grasses, sedges, and rushes, in species of the genus *Yucca,* in several caryophyllaceous plants (*Drypis* and *Acanthophyllum*), in *Acantholimon,* belonging to the order Plumbagineæ, and in some saltworts and succulent plants (*Umbilicus spinosus, Sempervivum acuminatum*). The green leaves are numerous, usually crowded thickly together to form a tuft, and project from the axis in all the directions of the compass; they are rigid, undivided, linear, round or triangular in cross section, and terminate in a sharp, strong, piercing spine. This form of leaf may be termed *acicular* (or needle-shaped). In many cases, at all events, such leaves have exactly the form of needles, and in regions where the unaltered products of nature are still preferably used as tools and utensils, they actually serve as needles. That plants possessing leaves with these needle-like

Fig. 114.—Acantholimon and spiny Tragacanth-shrubs on the elevated steppes near Persepolis in Persia.

points are excellently protected against the attacks of animals, scarcely requires to be proved more in detail; however, it might be indicated by special mention of two interesting examples. In the Southern Alps, in the neighbourhood of Monte Baldo, and on the opposite mountains behind Vallarsa, a species of grass (*Festuca alpestris*, see fig. 86 [5]), is found here and there, whose rigid leaves, projecting in all directions,

Fig. 115.—Group of Thistles (*Cirsium nemorale*).

terminate in needle-shaped points. This grass is the plant most detested in the whole district, and the shepherds try to destroy it by burning, wherever it appears in quantity, since the grazing animals, when seeking other plants growing between the patches of *Festuca alpestris*, cut their nostrils so severely that they often return from their grazing in a bleeding condition. It is remarkable that when these grasses can be easily uprooted, the grazing animals themselves bring about this destruction. The Mat-grass (*Nardus stricta*), when growing in the meadows, is seized low down

between the teeth of the oxen, torn from the ground, and dropped, so that it forthwith dries up and perishes. I saw thousands of the tufts, which had been rooted up by oxen, lying, dried and bleached by the sun, on the meadows on the Almboden of Oberiss, in the Tyrolese Stubaithal. It must not be supposed that the animals accomplish this clearance of the meadow deliberately; but it may indeed be admitted that they root up the patches of Mat-grass in order thus to obtain the

Fig. 116.—*Acanthus spinosissimus.*

enjoyment of the other plants growing between them, and avoid the risk in doing so of wounding their mouths with the pointed Mat-grass leaves.

A considerable proportion of plants with sharp acicular leaves inhabit steppes specially distinguished by the great dryness of their summer, particularly the elevated steppes of Persia, where they form a remarkable feature of the landscape. This applies most of all to the numerous species of the genus *Acantholimon*, a group of which, intermixed with spiny Tragacanth bushes, drawn from nature by Stapf, is exhibited in fig. 114. Like gigantic sea-urchins, lying strewn in groups on the sea-bottom, these plants, growing in hemispherical patches, live on the stony

soil of the elevated steppes, where they are so well protected by their needle-shaped leaves, projecting all round from the stem, that they are never eaten by grazing animals.

With the acicular form of foliage-leaves are ranked those which may be best compared to the process of the sword-fish. The outline of the leaves belonging to this form is linear, or linear-lanceolate, generally they are elongated, and often also slightly curved. Many of them are thickened and fleshy, but at the same time very hard and rigid on the outside. The points, produced by the terminations of the vascular bundles, spring from both margins of the leaf, and in the majority of instances stand at right angles to the margins; more rarely are they directed forwards. Each leaf either ends in a strong-pointed thorn, as in the agaves, or in a bundle of threads, as in *Bonapartea* and *Dasylirion*. The teeth on the leaves of the last-named plants remind one most in form, surface, and colour, of the scales of a shark, and can inflict frightful wounds on those who come too closely into contact with them. The table-land of Mexico is particularly rich in plants with leaves armed in this manner; that country is especially the habitat of agaves and Bromeliaceæ, of species of *Dasylirion* and *Bonapartea*. The Cape also is the home of a series of these forms, viz. those belonging to the genus *Aloe*. Species of *Eryngium*, with agave-like leaves (*Eryngium bromeliæfolium*, *pandanifolium*, &c.) belong to Mexico and South Brazil. It is worthy of note that several aquatic plants, such as *Hydrilla*, *Naias*, and the Water Soldier (*Stratiotes aloides*), have their leaves similarly armed, and are thus protected from the attacks of plant-eating aquatic animals.

A third form of foliage-leaf, armed with spines, is that of the thistle. The word thistle is here used in its widest sense, and is not restricted to species of the genus *Carduus* and *Cirsium* (see fig. 115). By the term thistle-leaves are indicated all those which are more or less lobed and divided, whilst the margins and the extremities of the lobes are provided with stiff, projecting spines. Such leaves are possessed by very many composites of the genera *Carduus*, *Cirsium*, *Chamæpeuce*, *Onopordon*, *Carlina*, *Echinops*, *Kentrophyllum*, *Carduncellus*, especially also in many Umbelliferæ (*e.g.* *Eryngium amethystinum*, *Echinophora spinosa*, *Cachrys spinosa*), some nightshades (*e.g.* *Solanum argenteum*, *pyracanthos*, *rigescens*), several Cycadeæ (*Zamia*, *Encephalartos*), and are very strongly developed in *Acanthus*, of which a species, *Acanthus spinosissimus*, growing in the Mediterranean floral district, is illustrated in fig. 116.

Nowhere in the whole world is the thistle-leaf met with so abundantly and in such manifold varieties as in the Mediterranean flora; Spain and Greece, Crete and Algeria, are particularly rich in districts covered with thistles. Thistle-leaves often appear divided into three, four, or five portions, and split up into numerous points, sections, and lobes. The ends of all the separate portions being transformed into stiff points, not much remains of the green tissue of the leaf; only a small narrow green lamina is seen, from which radiate out yellow and white spines on all sides, like lances of various lengths

Prickle structures, which are not to be regarded as metamorphosed terminations of leaf-ribs, but which originate from the epidermis of the leaf, are sometimes multicellular, sometimes unicellular. The former are termed prickles (*aculei*), the latter bristles (*setæ*). In this series of weapons, *barbs* are particularly worthy of notice. These are formed by obliquely directed conical cells, which project from the margin of the leaf, and terminate in a hard silicified, generally somewhat bent, apex (figs. 117 [7] and 117 [8]). Leaves, whose margins are thickly beset with these cells, exhibit, under the microscope, a saw-like appearance. It is

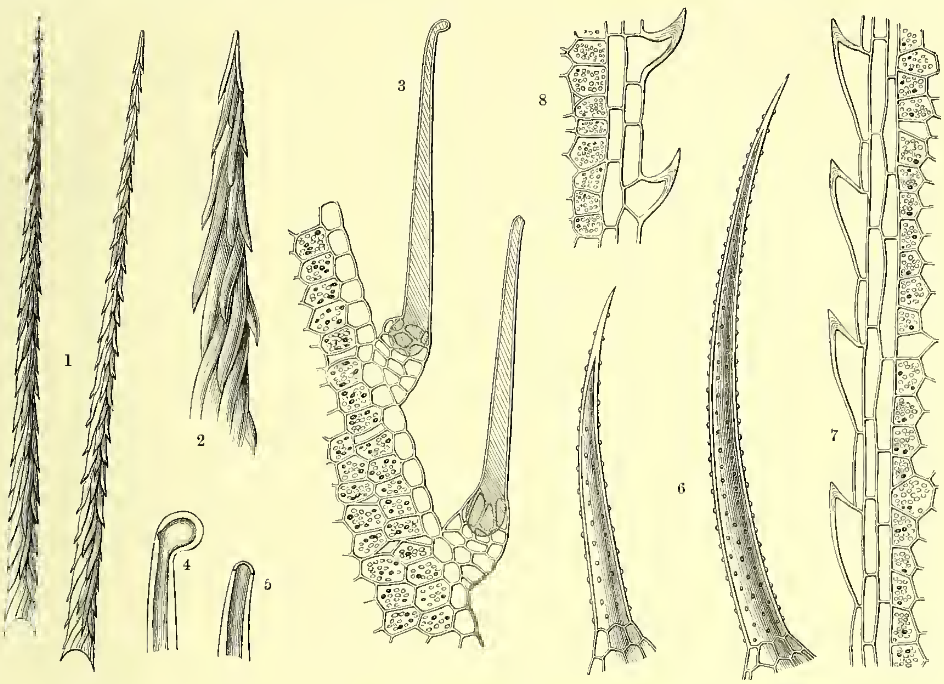


Fig. 117.—Weapons of Plants.

[1] Barbed bristles of *Opuntia Rafinesquii*; ×25. [2] Upper portion of this barbed bristle; ×180. [3] Vertical section through a part of the leaf, based with stinging hairs, of the Stinging Nettle (*Urtica dioica*); ×85. [4] Capitate termination of a stinging hair; ×150. [5] The capitate termination broken off; ×150. [6] Pointed bristles of *Echium Italicum*; ×40. [7] Margin of a scabrous leaf, beset with barbs, of a Sedge (*Carex stricta*); ×200. [8] Margin of a scabrous leaf, beset with barbs, of a Grass (*Festuca arundinacea*); ×180.

to be noted that leaves of this kind can, under certain circumstances, really act as saws. If such leaves are very gently stroked in the direction opposite to that of the points, they do not, of course, immediately cut the hand, but they do not bend, and under increasing pressure, the lamina of the leaf becomes arched. Since the leaf is also well stiffened, a resistance is encountered which could scarcely have been expected from so fragile a leaf. If a surface on which portions of these leaves have been laid be shaken, the bits move in a direction opposed to that of the points of the barbs. Movement in the opposite direction is impossible, because it is opposed by these apices. When such leaf-portions get into the mouths of ruminants, they can easily move forward to a particular

side, and in a particular manner, such as does not suit the purposes of the grazing animal, and is by no means welcome to it. By firmly stroking the margin of such a scabrous leaf, a wound is produced, the silicified points on the margin acting like the teeth of a fine saw. It is readily intelligible that grazing animals will shun such scabrous leaves; indeed, it is a matter of observation that they seldom (and then only when impelled by great hunger) eat sedges (*e.g.* *Carex stricta* and *C. acuta*), and those grasses which possess particularly sharp-edged leaves.

Still worse than the barbs of scabrous leaves are the barbed bristles (figs. 117 [1] and 117 [2]), which, it is true, but rarely occur in plants; indeed, almost exclusively on the branches of opuntias. They are always found surrounding the buds, which rise like warts, with fine bristles above the green tissue in opuntias or prickly pears. If such a spot be ever so lightly touched, small stiff bristles will certainly remain sticking in the skin of the hand, and will produce a very unpleasant itching sensation. On trying to pull out these small brown bristles the matter is only made worse, for they then penetrate much deeper into the skin, and may produce violent pain and inflammation. The reason of all this is at once evident on examining one of the bristles under the microscope. Each bristle is composed of numerous rigid, fusiform cells, arranged in spiral rows; at the upper end each of these cells is wedged in between the others, but the very hard, backwardly-directed, pointed end is free, and thus the whole structure is set with barbs. When once the point of the bristle has penetrated the skin, it is held there by the barbed cells. With the slightest pressure they are easily moved forward in one direction, but on trying to produce a movement in the opposite direction, the free ends of the cells resist the attempt, and it is unavoidable that the forcible extraction of one of these bristles should injure a larger area of the skin than would have been thought possible from the small size of the structure.

Another form of weapon originating from the epidermal cells consists of stiff hairs or bristles, with hard silicified cell-wall and sharp apex, which prick and wound like needles, though only unicellular; they are called pointed bristles. They usually project from the surface of the green leaves, closely crowded together, and their points are turned in the direction from which an attack might be expected. They appear gigantic in comparison with barbs, for even the smallest are much longer than these, and the largest resemble pins with their heads imbedded in the leaf-blade. This comparison becomes the more fitting since the pointed bristles are surrounded at their base by very regularly arranged cells which rise above the surface like a cushion, or often like a short white cone. The bristle itself on the end of this pedestal is formed of a single cell, which, when fully developed, loses its protoplasm and becomes filled with air. The wall of this elongated cell is hardened by the deposition of silica, and is usually unequally thickened by small knobs (fig. 117 [6]). Although pointed bristles are developed in numerous groups of the vegetable kingdom, one group is especially so armed.

This is the family of the Boragineæ, which has been thus named, indeed, in consequence of its characteristic armour. Examples of the equipment described are furnished in abundance particularly by species of the Viper's Bugloss (*Echium*), from which the pointed bristles in fig. 117 [6] are taken, and of the genera *Onosma*, Comfrey (*Symphytum*), and Borage (*Borago*).

On the leaves on Nettles, Loasaccæ, Hydrophylleæ, and Euphorbiaceæ, occurs a very peculiar mode of protection against the attacks of large herbivorous animals, in the formation of stinging hairs or bristles. These stinging hairs are formed of single large cells like the pointed bristles of Boragineæ. They expand like a club at the lower end, and are much elongated above. Only in *Wigandia urens*, which belongs to the Hydrophylleæ, is the upper free end finely pointed; in the species of the genus *Jatropha*, in Loasaceæ, and in nettles, the extremity is swollen into a small head, which is bent to one side. At the knee-shaped bend the cell-wall of the stinging hair is extremely thin (figs. 117 [3, 4, 5]), so that the slightest contact suffices to break off the head. As the head is broken off obliquely, a very sharp point is produced, and the opening formed by the rupture is not horizontal, but oblique, so that the broken end resembles the poison-tooth of a snake or the nozzle of a hypodermic syringe. The breaking, independently of the extreme thinness of the cell-wall below the head, is helped by the brittleness of the hairs, and this is caused by the silicification, sometimes by the calcification, and in *Jatropha* by the lignification, of the cell-wall. This modification of the cell-wall, however, is restricted to the upper part of the hairs. The cell-wall of the club-like swelling at the base of the stinging hair is neither silicified nor calcified, but consists of unaltered cellulose, and yields to an external pressure, so that by such a pressure the outflow of the cell-contents is assisted. By these means, also, the stinging hair is enabled to become turgid, which property certainly plays a very important part in the outflow or outspurt of the cell-contents from the silicified or calcified funnel-shaped apex after the head has been broken off. When by a pressure from above the brittle end of the hair is splintered, and the head broken off, the point formed at the place of rupture penetrates into the body causing the pressure, provided this is soft, as, for example, the skin of men and animals; and the contents are injected into the wound so formed. In the fluid contents of the stinging hair a substance occurs together with formic acid, resembling the unorganized ferments or enzymes, and it is this which produces the violent inflammation round the wound formed by the puncture. The painful sensation felt immediately after the puncture, which is popularly called "burning", on account of its resemblance to that produced by a burn, is indeed caused by the formic acid; but a series of other phenomena which are observed after the puncture, can only be placed to the account of the enzyme, which acts like a poison. When numerous stinging hairs penetrate the skin in close proximity, a wide area becomes reddened, and inflammatory swellings, with violent pain, are produced. Even the European nettles, viz. *Urtica dioica* and *urens*, give rise to unpleasant burning and

itching, and very severe attacks, tetanus, &c. are produced, as by snake-bites, by the *Urtica stimulans* of Java, the *Urtica crenulata*, which is a native of India, and the *Urtica mentissima*, growing in Timor. Generally, an analogy between stinging hairs and the hollow poison-fangs of snakes cannot fail to be recognized.

The mass of tissue in which the stinging hair is imbedded consists of chlorophyll-bearing cells, and is elastic and flexible; whenever a stinging hair is pressed on one side it lies close to the leaf-surface, so that the point does not penetrate the skin of the fingers pressing it, and does not form, or poison, a wound. When the pressure is removed, the hair becomes erect again in virtue of the elasticity of its knob-like support, and directs its brittle point outwards. Upon this fact depends the trick of stroking a nettle with the hand so as not to be stung. The lower, unarmed part of a leafy nettle, whose foliage is beset with innumerable projecting stinging hairs, is taken in one hand, and the other hand is then passed from below upwards over the foliage, and in this way the hairs touched are pressed on to the leaf surfaces and do not wound. But if the nettle is touched from above, the heads of the hairs are immediately broken off, the perforated points penetrate the skin and discharge their poisonous fluid into it. Grazing animals carefully avoid plants furnished with stinging hairs, and do not let their nostrils, nor the mucous membrane of their mouths, get poisoned by the corrosive fluid. The nettle is, therefore, well protected against larger animals. Their foliage is, indeed, eaten by the larvæ of *Vanessa Urticæ* in spite of the stinging hairs, but this injury is restricted to only a portion of the leaves; they can always develop new leafy shoots from the intact stems and buds, and, at any rate, the nettle does not perish on account of the ravages of these larvæ.

This is also the most suitable place for the consideration of a form of plant-hair, whose cells, indeed, possess no stiff silicified walls, and which, therefore, do not prick and wound, but which, nevertheless, keep the plants they clothe from injury by grazing animals, and which thus far must also be regarded as agents for protecting the green tissue. These hair-structures have already been described when making clear the protection afforded to leaves against excessive transpiration. Such hairs, as we saw, are particularly well shown by many species of the genus Mullein (*Verbascum*). These branched, radiating hairs, reminding one of tiny fir-trees, are easily detached from the surface of the leaves from which they spring, and a very slight pressure of the hand is sufficient to lift off numerous flocks of this hair-felt. Although the cells which build up the hairs of the leaf-felt are not stiff and prickly, and do not penetrate into the skin, they very readily remain hanging to the smallest inequalities on the surface of the disturbing body. If grazing animals bring the mucous membrane of their mouths into contact with the leaves of the Mullein, this mucous membrane immediately become covered with flocks of the detached hair-felt, which establish themselves in the inequalities of the surface, and they certainly produce anything but a pleasant sensation. On the peculiar adhesion of the felt-hairs of the

Mullein to the mucous membrane rests the necessity for the caution which people observe in the preparation of Mullein. The flowers of the Mullein (*Verbascum thapsus*) have been used from time immemorial in the preparation of a tea. When hot water is poured over the flowers, which are covered on the under side, just like the foliage-leaves, with a fine felt of hair, portions of the felt are detached, and remain floating in the infusion. If the decoction is not filtered through a piece of linen, some of the hairs may stick to the mucous membrane of the mouth, and there produce an intolerable irritation and itching. This unpleasant sensation is certainly much more powerful in animals when taking the leaves of Mullein in their mouths than with us when we drink unfiltered mullein tea, and it no doubt deters animals from eating the foliage of the plants in question.

The protective mechanisms just described are all borne directly by the particular organs needing protection. But there are many plants whose foliage is unequipped with armament of this sort, and in which adjacent parts of the plants afford the protection. One may instance all such plants as have soft, unarmed leaves, sheltered from attack by lateral shoots transformed into spines. The stem and branches of these plants are not clad with foliage entirely to their summits. The ends are usually leafless, and look as if their leaves had been stripped off. Generally speaking, if leaves are present on the summits of the branches, they are stunted, small, indicated only by scales and protuberances, and are anything but an attractive food. Consequently, the end of the woody branch appears tapering, and terminates in a stiff, sharp spine. In a bush whose branches project out in all directions with leafless apices, while their green foliage-leaves are collected behind the apex, a most efficient system of defence is produced, resting upon division of labour. The green leaves can carry on the work assigned to them undisturbed under the protection of the spines, and if it happens now and then that a large food-seeking animal, driven perhaps by greed or hunger, pushes his mouth carefully between the confronting spines, and knows how to procure some green leaves from behind the spines, the existence of such a bush is not seriously threatened. The Alhagi shrubs of steppes, as well as several brooms and *Cytisus* shrubs, viz. *Alhagi Kirgisorum*, *Genista horrida*, and *Cytisus spinosus* (fig. 118 [5]), exhibit the protective mechanisms just described in a marked manner. In many other shrubs, such as sloes, sea buckthorns, and buckthorns (*Prunus spinosa*, *Hippophaë rhamnoides*, *Rhamnus saxatilis*), the same contrivance is indeed met with, but it only has the full significance while the foliage-leaves are quite young. Only so long as the tender leaves, which have just emerged from the buds, are overtopped by the spiny branches are they protected from being devoured; afterwards when they have developed, those only are protected which clothe the base of the spiny branches. On the long axes of the Hawthorn, in the axils of the lower foliage-leaves, there are always developed, close together, a long spine and a small bud, in the axils of the upper leaves a bud only. In the following year, reduced axes develop from the buds situated close to the

long, shiny, brown spines, which often bear flowers; but from the buds on the upper half of the shoot, a long axis arises, which repeats the development just described. Spines, which on the American species of hawthorn, become in *Cratægus coccinea*, 4 cm., in *C. rotundifolia*, 6 cm., and in *C. Crus galli*, 7–8 cm. long, resemble sentinels which have to protect these developing reduced axes. Most of these bushes develop horizontal projecting branches, and therefore extend as far transversely as vertically, and since the spines remain for many years, the leaves of all these axes, which, in later years, spring laterally from the branches, almost in the interior of the bush, behind the old spines, are protected by them. In several Brazilian mimosas, the spines situated on the branches do not indeed project beyond the outspread leaves, but as soon as animals disturb the leaves, they are revealed from their concealment behind the protective defence of spines, and the animals retreat before the sharp points now confronting them.

A very peculiar relation is observed between green leaves and spines in most of those semi-shrubs which Theophrastus in olden times grouped together under the name of "Phrygana". In these semi-shrubs, of which the *Vella spinosa*, represented in fig. 118 [8], may be selected as an example, each shoot growing out from the winter buds develops green foliage-leaves on the lower half and above these, and frequently also in the region of the inflorescence, green lateral twigs transformed into sharp-pointed spines. These spines, which, in many instances, as when they appear in the region of the inflorescence, may be considered as metamorphosed flower-stalks, are at first soft and succulent, contain green tissue in their cortex, and function at first exactly like the narrow foliage-leaves situated near them. In the first year they play no part as protective agents on account of their softness; in the autumn, the green leaves fall from the shoots; the spinous tips of the branches are also dead and withered, but they still remain, and do not fall off. During the summer, having become hard and stiff, they now wound anyone who seizes them roughly, and obviously protect the shoots which spring from the lateral buds in the following year behind their dried-up ends, in which the development just described is repeated. Thus arise, in time, bristling shrubs, from whose periphery radiate out a quantity of dried-up spiny branches, and which often look as if the branches had become frozen and shrivelled in the winter, and as if the whole plant were in a dying condition. This "Phrygian" underwood is not certainly an embellishment of that region in which it occurs in masses, but it forms a highly characteristic feature in certain floral districts. The Mediterranean area is particularly rich in these "Phrygian" bushes, and species belonging to the most diverse families develop in this form. To mention only a few examples, of Cruciferæ, *Vella spinosa* and *Koniga spinosa*, of Rosaceæ, *Poterium spinosum*, of papilionaceous plants, *Genista Hispanica* and *Onobrychis cornuta*, of Compositæ, *Sonchus cervicornis*, of Euphorbiaceæ, *Euphorbia spinosa*, of saltworts, *Noëa spinosissima*, and of Labiateæ, *Teucrium subspinosum* and *Stachys spinosa*, may be pointed out. The elevated steppes of South-west Asia also exhibit Phrygian forms, and indeed, chiefly, as isolated,

prickly, and spine-stiffened, low bushes, growing together with thorns, and low Tragacanth-shrubs, in which the green foliage is protected differently. In northern regions not exposed to summer drought, where grazing animals find in summer enough green fodder, this form of plant is almost entirely absent. It is only met with in the heaths and pine forests of Central and Western Europe, in some species of broom (*Genista Germanica* and *Genista Anglica*).

In these regions, certain shrubs and young trees, which do not possess the spine formation described above, acquire from the grazing animals themselves a shape which strongly resembles the Phrygian form. It is brought about in the following manner. If young trees of beeches, oaks, and larches, or bushes of Ling (*Calluna vulgaris*), are accessible to goats, sheep, and oxen, these bite off the ends of the fresh shoots, together with the leaves attached to them. The remaining portion of the mutilated shoot in the neighbourhood of the wound dries up, but the part behind keeps alive, and the buds on it develop even more vigorously than would have been the case if the mutilation had not occurred. The shoots which in the following year arise from these buds, however, may suffer the same misfortune; they may again be pruned by grazing animals, and when this is repeated every year, the mutilated beeches and larches at length come to resemble the beeches and larches of old French gardens, which have assumed the shape of pyramids and obelisks in consequence of the continual clipping of the gardener's shears. The branches of these small mutilated trees become so thick, and the dry, hard twigs on the periphery of the crown are so crowded together, that even the greedy goats are prevented from breaking through the armour, and abstain from pulling out the green shoots from behind the dry stumps. Thus at length the unprotected plants obtain a defensive armour which is capable of saving them entirely from the further attacks of grazing animals. Many of these young mutilated and bitten trees, of course, never develop into strong lofty specimens; but in some species the rough treatment which they undergo in their youth does not result in lasting injury. This applies especially to larch-trees growing in Alpine valleys. The young trees gradually form thick branched bushes in their struggle with the goats, and a top cannot be definitely distinguished in them, since the central shoots, as long as they can be reached by the goats' mouths, are not spared. But, at last, after a number of years, the bushy larches attain to such a height and circumference, that the goats can no longer reach the upper shoots. And behold, a strong shoot arises from the middle of the much-branched bush, develops a whorl of lateral branches, elongates from year to year, and being no longer harassed by the grazing animals, grows up into a lofty larch-tree. For a long time, at the lowest portion of the tree, may be seen projecting the oldest lateral boughs, which have become abundantly branched in consequence of the mutilation, and which serve to protect and defend the developing central stem. But gradually these lower branches decay, and fall crumbling on the ground; thus the last reminiscence of their severe youth is obliterated.

The contrivance for protecting the green tissues of the cactuses, depending upon a division of labour, is accomplished in a very peculiar way. Our conception of a plant is a stiff grey or brown stem bearing soft green leaves. In the cactus-like plants, however, the most important types of which we have already recognized in the Cactaceæ of the New World, and the columnar Euphorbiaceæ of Southern Asia and Africa, everything is reversed. Here the stem is green and succulent, and the leaves it supports are transformed into stiff grey or brown spines. Food is conducted to the green transpiring tissue in the cortex of the stem, in which, and not in the leaves, new organic materials are produced. The leaves which have been changed into spines, on the other hand, have to keep guard that the green tissue in the cortex of the columnar or flattened stem is touched no more than is necessary. This reversed state of things strikes us as most strange in the opuntias (Plate IV.), because here the portions of the stem have the form of thick elliptical leaves, and consequently are usually held by non-botanists to be leaves. But the spines, or, strictly speaking, the leaves transformed into spines, occasionally attain to an extraordinary length in these opuntias. They are 3–5 cm. long in *Opuntia Tuna, decumana,* and *magacantha,* and even 8 cm. in *Opuntia longispina.* It has already been mentioned that the buds of opuntias are based with very small barbed bristles, and consequently these plants are armed with a twofold defence against possible attacks with large spines, visible from afar, and with these horrible small inconspicuous barbed bristles. In the cactus-like plants the variety of weapons is very great, and if all the various forms of long and short, thick and thin, knotty and smooth, straight-pointed and barbed, arched and wavy spines and bristles were placed together side by side, quite a goodly collection of arms would be the result. A single species often bears three or four kinds of weapons, and these are arranged and distributed in a great variety of ways, and in this respect a diversity is developed which has a fascinating effect on anyone who has an inborn taste for such changes of form, and we can understand how it is that so many lovers of flowers have devoted themselves to the study and culture of these curious representatives of the vegetable kingdom. Although it is impossible to show the connection between the kind of armour and the attacks to be warded off in each individual instance, even the most cursory glance shows us that the points of the spines, however these may be shaped and arranged, are always placed in front of that portion of the stem which is best furnished with green tissue. In the columnar euphorbias, *e.g.* in *Euphorbia cœrulescens,* the stems are furnished with shallow longitudinal grooves clothed with green tissue. On the ridges between the grooves are inserted pairs of divergent spines with their points in front of the grooves, and thus ward off every assault on the green tissue. Exactly the same thing is seen in the columnar *Cereus,* and in the cone-shaped *Echinocactus* and *Melocactus.*

On looking at these columnar, flattened and spherical cactuses, the question arises whether it is necessary for them to be surrounded with such a complicated

PRICKLY-PEARS ON THE PLATEAU OF ANAHUAC (MEXICO).

Printed from the originals by the BIBLIOGRAPHISCHES INSTITUT, Leipzig.

system of spines. According to the ordinary conception of the method of feeding of the herbivorous animals referred to, it would be thought that these green clumps, pillars, and balls, even without their terrible equipment, would form anything but choice food. But when they are seen in their original habitats, it is easily seen that they have every need to protect themselves and to defend their existence. While on the stony and sandy plains and slopes which form the habitat of cactuses, all other plants have long been withered, and a green leaf can no longer be seen for far and wide, when all the springs of water are dried up, and not a drop of rain has moistened the ground for months—then the cactuses still remain always fresh and green, and by the assistance of their central aqueous tissue, they are able to survive through the greatest drought and aridity which are ever observed on the earth. But at such periods of drought, every cactus-ball appears like a cordial to the hungry and thirsty animals, and frequently even as the only alternative to death. In spite of the frightful spines with which species of *Melocactus* are bristling, these are sought by the wild asses in the plains of South America at the periods of greatest drought, and are rooted up where possible by their hoofs in order to get at the juicy tissue of the unarmed lower parts; or the animals try to split the cacti with their hoofs, and in this way to get at the interior, in which proceeding it very often happens that the assailants injure themselves by the spines and receive dangerous wounds.

Next to the cactuses, the strangest spine-formations are exhibited by the low half-shrubby tragacanth bushes (Astragali) belonging to the group *Tragacanthacei*, which, in an inexhaustible variety of species have their habitat throughout Southern Europe, but chiefly in the east, on rocky mountains and elevated steppes. We will pick out one, viz. *Astragalus Tragacantha*, from the large number of species, and explain by words and picture the remarkable protective contrivance of its green foliage-leaves (fig. 118 [1]). On observing this plant very early in the spring, a tuft of numerous long, dry, grey spines, whose points are directed upwards and outwards, is seen on the free extremity of each branch. In the centre of this tuft of spines lies a bud, which forms the top and termination of the branch in question. The warmth of spring causes this bud to develop, and the close-pressed pinnate leaflets become loosened, stretch out, and unfold; but weeks pass by, and the leaflets are always still surrounded by the bushy garland of spines. Their green colour can only be seen shining through from behind the long spines as from behind the grey lattice bars of a cage. When they are fully developed, and when they have also somewhat lengthened the branch they adorn, the uppermost leaflets at length project beyond the points of the spines. But see—the end leaflet which had been situated on the rachis of the pinnate leaf has already dropped off, and often a pair of the lower leaflets with it (fig. 118 [2]), and all that now projects beyond last year's spines has also become changed into a spine. The rachis of the leaf at the point where the terminal leaflet was formerly inserted becomes hardened and transformed into a pricking point. Then comes autumn, the period of the leaf-fall.

Most deciduous shrubs now throw off the leaves with which they have worked all the summer, by means of the formation of a layer of separation at the place where the leaf is inserted on the stem, as previously described. But this does not occur in the tragacanth bushes. Only a portion of the long grey spines by which this year's leaves were surrounded are cast off. The leaflets of the present year are now detached from the leaves; the strong midribs or axes whose ends had already become changed into spines during the summer remain firmly joined to the stem and dry up, forming thus a new stiff tuft of spines which is as like the one thrown off as one egg is to another. Accordingly the dried-up remains of the leaves of one year, now changed into spines, become an apparatus for protecting the developing green leaves of the year following. Observation in the natural state shows that these projecting spines are capable of protecting the green leaves behind them from the attacks of grazing animals. One may see how grazing animals stop in front of the shrubs bristling with spines, and actually abstain from further attacks after the first attempt, although the foliage of the tragacanth named, like that of other papilionaceous plants, would furnish a very desirable meal.

Different from the Tragacanth is the Barberry (*Berberis*). On looking in summer time at a shoot in vigorous growth, it will be seen to be beset with two kinds of leaves: first, with leaves which have anything but the appearance of foliage, being transformed entirely into spines like those of the cactuses. These at the base of the shoot are drawn out into from five to seven, and further upwards into three, needle-shaped points, as shown in figs. 118 6 and 118 7. Short branches beset with ordinary green foliage-leaves arise simultaneously in the axils of these metamorphosed leaves. These short branches terminate in buds which develop early in the following year, and then form either flowers, or long branches. The foliage-leaves of the short branches, below these buds, fall off in autumn. The three-pronged spines at the bases of the short branches, *i.e.* of the buds which have passed through the winter, remain behind, and radiate out from the shoot with their three needles in three directions. Now, when in the following spring the buds at the end of the short branch swell, and young tender foliage-leaves burst from them, these are excellently protected against being devoured as long as the points of the three-pronged spine still project beyond them.

In *Robinia Pseudacacia,* popularly known by the name of Acacia, and also in numerous other robinias as well as in several Siberian caraganas (*Caragana microphylla* and *pygmæa*), the stipules are transformed into prickles, and not, as in *Berberis,* the whole leaf. In all Leguminosæ, structures arise right and left of the place of insertion of the leaf on the stem, known as stipules (*stipulæ*), on account of their position. They are not leaf-like in the robinias and shrubs named, but are transformed into brown spines drawn out into a sharp point. When the foliage-leaf becomes detached and falls off in autumn, both the spinous stipules remain behind and persist even on into the following summer. In the axil of the two divergent spine-stipules is situated a bud which unfolds in the following spring. Here we have again repeated the same protective mechanism as was previously

sketched in the case of the Barberry. As long as the young tender foliage-leaves remain in this situation between the two spiny stipules (fig. 118 [4]) they are avoided by animals; the protection is only at an end when they have grown beyond the points of the old spiny stipules.

Most of the last-described protective contrivances only defend the green foliage

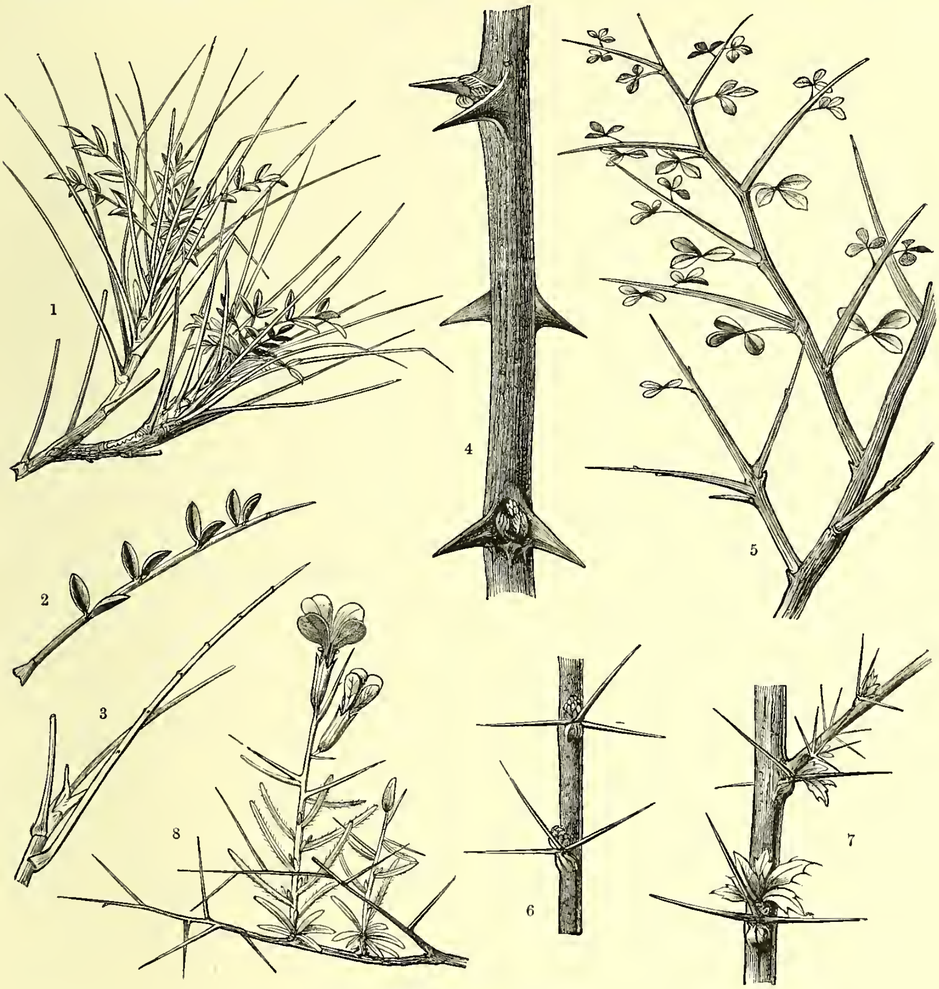


Fig. 118.—Weapons of Plants.

[1] Branch of the Tragacanth bush (*Astragalus Tragacantha*) in spring. [2] A single leaf of this Tragacanth from which the three upper leaflets have fallen. [3] Leaf-axis from which all the leaflets have fallen. [4] Portion of a shoot of *Robinia Pseudacacia* in spring. [5] The spiny Cytisus (*Cytisus spinosus*). [6], [7] Portions of branches of the Barberry (*Berberis vulgaris*) in spring. [8] *Vella spinosa*; the end of last year's shoot is dried up; this year's shoot bears flowers.

whilst it is young. But this is exactly the time when protection is most needed. If, later on, isolated foliage-leaves, which have grown beyond the points of the prickles, are eaten, this does not so much matter, as part of the foliage still certainly remains, and this is really the important point.

From the fact that the protection of the young green leaves is secured by

a portion of the old dead leaves, by dried-up structures of the previous year, in tragacanth bushes and also in many caraganas, and generally in numerous other plants, two things may be learned: first, that one and the same plant-member may in the course of a year change its function; and secondly, that dead, withered portions are often called upon to play an important part in the life of a plant. The same thing is frequently observed in flowers and fruits. It often happens, for example, that floral leaves, which originally served to allure insects and to protect the pollen from moisture, are of use later on when dried, in the dissemination of the fruits and seeds. In foliage-leaves, on the other hand, such a change of function is comparatively rare, and is hardly ever observed except in the plants of steppes and of the Mediterranean flora.

It would naturally be expected that the protective contrivances required by the green tissue against an excessive destruction by animals, would also exercise an influence on the gregarious growth of plants as well as on the dwelling together and distribution of plants and animals; and this is proved by numerous observations. Let us suppose ourselves in a country where plants of a hundred different kinds grow up side by side. The shrubs, bushes, and herbs, mixed together, contain the most diverse substances. Some abound in milky juices; others are as bitter as gall; whilst others again taste frightfully sour or contain in their sap alkaloids, the partaking of which would be deadly to many animals. Here is a plant armed with stinging hairs; there from a bush radiate out innumerable spines; and again in other places thistles rear their prickly leaves. The one prevents snails from eating the foliage, the other caterpillars or grasshoppers; a third, goats; a fourth, horses, &c. Let it be supposed that the country producing this rich vegetation is temporarily quite shut off from everything which creeps or flies. But now arrives a numerous herd of some species of animal against whose attacks one portion of the plants is protected as completely as possible, a second portion only partly, a third not at all. What will be the consequence? The last will be wholly or partly devoured, while the first will remain uninjured. If this is often repeated, at last the one will vanish from the scene, while the other will develop in overwhelming quantity. But in this manner the peculiar composition of vegetation in places where grazing animals regularly appear is naturally explained.

It must strike everyone who visits the Alps that in the neighbourhood of the cow-chalets a luxuriant vegetation springs up from the richly-manured soil, very tempting in appearance, but nevertheless left unattacked by the grazing animals. The shepherds do not prevent the animals from eating of this luxuriant growth; it is not necessary, for instinctively they detest these plants. The bush consists entirely of species which are poisonous or disagreeable to the animals, or which when disturbed, wound them—viz. of Monkshood, Good King Henry, Nettle, and Fuller's Thistle (*Aconitum Napellus, Chenopodium Bonus Henricus, Urtica dioica, Cirsium spinosissimum*), which are found together here, and have developed so much the more vigorously, since the other species originally existing (which were innocuous and undefended) have been long ago destroyed by the grazing animals.

On the forest pasture of the Lower Alps often all that is to be seen covering the ground are mosses and ferns, which are offensive to the animals, along with the bitter *Gentiana asclepiadea* and *Aposeris fœtida,* abounding in a malodorous milk, detested by all ruminants. In some meadows in the Central Alps the fern *Allosorus crispus,* and with it the Mat-grass (*Nardus stricta*), are so prominent that scarcely any other species of plant are to be seen there. Again, in other places, the ground is overgrown with the Bracken fern (*Pteris aquilina*), detested by grazing oxen, and also with prickly juniper-bushes. On the cultivated grounds near Trieste the stiff, prickle-leaved and steel-blue Eryngium (*Eryngium amethystinum*) impresses one by its profusion. In the Hungarian uplands one may recognize the spots where cattle are kept by the abundant occurrence of *Xanthium spinosum* and *Eryngium campestre,* of tall thistles and of Mullein, of Thorn-apples and Henbane, and of several species of spurge, which are only eaten by the animals under the greatest stress. It is thus shown by a hundred examples that in tracts exposed to the pasturage of larger animals, those plants always obtain the upper hand which are not attacked by the animals, in consequence of their poisonous and disagreeable properties, or because of their defensive spines and prickles.

A phenomenon connected with the conditions here described deserves mention. This is the regular occurrence of defenceless plants under the protection of those which are provided with abundant means of defence. Thus certain wild vetches and Umbellifers (species of *Vicia, Lathyrus, Anthriscus, Myrrhis, Ægopodium, Chærophyllum,* &c.), which would furnish very good fodder for grazing mammals, are regularly seen in the prickly hedges along the roads, and under spiny bushes, which form a belt around forests. The bushes defend not only their own foliage, but also that of the delicate vetches and Umbellifers which have established themselves under their protection. In neighbourhoods where the primeval character and distribution of the vegetation is almost entirely lost, the companionship of certain plants is so general that one might be tempted to regard it as a symbiosis. Here, however, this is certainly not the case, for the advantage is all on one side—that of the plants protected; while the bush, armed with spines against the assaults of animals, under whose branches the defenceless plants have grown up, receives no thanks, no profit, and no return from them, and certainly does not afford the protection intentionally.

METABOLISM AND TRANSPORT OF MATERIALS.

1.—THE ORGANIC COMPOUNDS IN PLANTS.

Carbon Compounds.—Metabolism in Living Plants.

CARBON COMPOUNDS.

It is naturally to be expected, from analogous relations in the inorganic world, that the variety to be observed in the vegetable kingdom as to colour, taste, and smell, should depend upon the diversity of the materials manufactured in the individual species. Numerous characteristic materials have been shown by the researches of chemists to belong to certain species, and in the names given to many of these (as in the terms oxalic acid, benzoic acid, salicin, amygdalin, asparagin, nicotin, strychnin, atropin, cocain, &c.) we recognize the names of well-known plants. But it would be erroneous to suppose that the series of substances belonging to the vegetable kingdom would be exhausted by the sugars, acids, salts, alkaloids, oils, ethers, and pigments which are already known to us by their varied effects on our nerves of taste, smell, and sight. What is accurately known, indeed, in this respect is apparently only a fraction of what actually exists. In the meantime we cannot venture on even an approximate estimate of all the substances produced by plants. Only this much can be affirmed with certainty, that their number is far greater than that of inorganic or mineral bodies. This is the more remarkable, since the elements of which the inorganic compounds are built up are comparatively so many, whilst the elements which serve as building materials for organic compounds are so few. The fact is thus explained, that carbon, an element whose chemical nature admits of its union with other elements in inexhaustible combinations, appears as the centre of all organic compounds in plants.

For the purpose of the following discussion it is fitting, first of all, to give here a brief sketch of this important property of carbon. Chemists call carbon a *tetrad* element, by which is meant that each atom of carbon enters into combination with four atoms of another element, and can form a mechanically inseparable group, *i.e.* a molecule. It can be shown that each atom of a tetrad element possesses four centres of attraction, *i.e.* four connection points, to which the atoms of other elements become attached, and where they are held fast. These points are called *bonds of union*, and are said to be *saturated* when other atoms have become

annexed or united to them, or *free* when this is not the case. When, for example, four atoms of hydrogen unite with one atom of carbon (represented graphically in figure 119, with its four bonds of union), its four bonds are thereby saturated, and a molecule known as *marsh gas* is produced. Apart from its tetravalency, carbon also has this remarkable property, that its atoms can also combine with each other, and to a much higher degree than the atoms of any other element. Carbon atoms themselves, and not the atoms of other elements, saturate the separate, free bonds of union in such instances, and in this way are produced groups of atoms, each of which behaves like a chemical unit. Suppose that one of the four bonds of an atom of carbon has united with one of the four bonds of a second carbon atom; then a group of atoms like that shown in fig. 120 will be the result. Where the two carbon atoms have become connected their bonds of union are saturated; but in each atom there are still three unsatisfied bonds, and accordingly they can together annex six atoms of another element. The pair of carbon atoms may now be considered as hexavalent, and if they annex six atoms of hydrogen, a compound is produced which is called *ethane*. If three atoms of carbon combine together, so that one bond of each is united to a bond of the neighbouring atom, as represented graphically in fig. 121, four bonds are saturated and eight remain free. These free bonds may be satisfied with atoms of other elements, for example, again with hydrogen. Thus a compound arises which contains three atoms of carbon and eight of hydrogen, and which has been called *propane*. In like manner four, five, &c. atoms of carbon may enter into combination together, in which case the remaining ten, twelve, &c. bonds of union, which remain free, may be saturated with atoms of other elements. If we suppose that all the free bonds are satisfied by hydrogen, we then have a series of *hydrocarbons* whose successive members differ from their predecessors by the increment of one atom of carbon and two of hydrogen, but which must each be regarded as a chemical unit, *i.e.* as a chemical individual and as a particular substance with peculiar properties not possessed by the others.

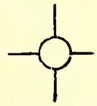


Fig. 119.

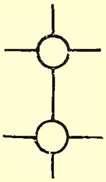


Fig. 120.

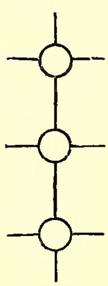


Fig. 121.

Parallel with this series of hydrocarbons run two comparable series, whose members respectively contain two and four atoms of hydrogen less than the corresponding members of the main series; and here the carbon atoms, from which the atoms of hydrogen have been removed, must have combined with one another by the bonds thus liberated.

The view that several atoms of carbon are only grouped in one direction in linear series, and that the neighbouring atoms are only mutually combined by means of one of their four bonds, as shown in the above graphic representations, is not always confirmed. In many instances we are obliged to suppose that the carbon atoms are distributed in several directions in space, and are combined into a net-work, or grouped in the form of a hexagon, perhaps in the manner illustrated

in fig. 122. Here each of the six carbon atoms is always united to one of its neighbours by one, and to the other by two, bonds, and thus only six bonds remain free. When these are saturated by atoms of hydrogen, we have a molecule of that important compound called *benzene.* In all the special instances hitherto mentioned the free bonds of the carbon atoms have been satisfied by atoms of hydrogen, and these combinations have all been found actually realized in nature. It is an extremely important property of carbon, as regards the chemistry of vegetable substances, that all the free bonds of its groups of atoms, no matter how numerous these may be, can be satisfied with hydrogen. Whilst other elements can only form a very limited number of hydrogen compounds, we have a practically unlimited quantity of hydrocarbons. But this is not all. These hydrocarbons form the foundations of innumerable other compounds which are produced by the displacement, by atoms of other elements, of one or several atoms of hydrogen in each member of the hydrocarbon series. Many of the substances occurring in plants are hydrocarbons in which a part of the hydrogen has been displaced by oxygen; in others the hydrogen is partly replaced by nitrogen; or for the hydrogen may be substituted the so-called compound radicles (groups of atoms which play the part of an element in combination), as, for example, cyanogen, hydroxyl, &c. If the number of compounds in which carbon is combined with nitrogen is indeed large, the number of compounds obtained from them by the partial replacement of the hydrogen by some other element, and known as *derivatives of hydrocarbons,* becomes almost beyond conception.

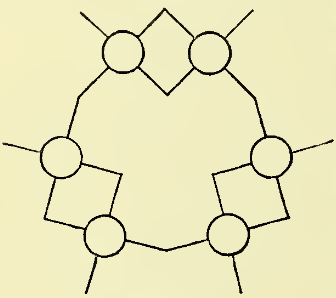


Fig. 122.

Finally, the astounding variety which one and the same compound can exhibit in its outward appearance, in form, colour, hardness, and transparency, in taste, and in smell, is due to the inexhaustible permutations in its percentage composition, which is shown by the hydrocarbons as well as by their derivatives. The same phenomenon is here repeated as is observed in pure carbon uncombined with any other element. It is known that carbon appears either amorphous as charcoal, or crystalline as diamond, or as graphite—in the latter case, in crystals which belong to another system than those of the diamond, and differing from them in colour, hardness, and specific gravity. It is not easy to imagine a greater contrast as regards physical properties than that shown by these three substances, and yet it is beyond question, that, chemically, they are identical. The same thing happens in some of the compounds of carbon. Dextrin, starch, and cellulose all have, for example, the same percentage composition; each molecule contains six atoms of carbon, ten of hydrogen, and five of oxygen. And yet how different these bodies seem to our senses; how different is their behaviour to heat and light, to various solvents, and to other chemical compounds! We explain this remarkable phenomenon by the way in which the atoms are

grouped, and imagine that the varied arrangement of the atoms building up a molecule finds expression in the whole mass of the substance in question. If six black, ten blue, and five red balls are placed close together in a frame, they can be grouped in the most diverse ways into beautiful symmetrical figures. They are always the same balls, they always take up the same space, and yet the effect of the figures produced by the different arrangements is wholly distinct. It may be imagined, similarly, that the appearance of the whole mass of a carbon compound becomes different in consequence of the arrangement of its atoms, and that not only the appearance, but even the physical properties undergo very striking alterations.

A glance back at the history of the development of carbon compounds, very briefly stated here, will render sufficiently clear how it becomes possible that many thousand different organic substances are compounded from carbon and a few other elements, viz., hydrogen, oxygen, and nitrogen; and how this almost infinite multiplicity of vegetable organic compounds is connected with the remarkable chemical nature of carbon. The materials of which these substances are formed are extremely simple, and the changes undergone by plant-substances depend entirely upon the insertion and rejection, on the grouping and arrangement, of the atoms of a few elements.

METABOLISM IN LIVING PLANTS.

In the living plant these combinations, decompositions, and rearrangements are accomplished with great ease, and multitudes of substances, which cannot be manufactured, either directly or indirectly, in a chemical laboratory, are produced in plant cells, with a hand's turn, so to speak. This applies principally to those organic materials already generally described in a previous section of this book, which have been formed from inorganic food, from carbonic acid and water. It is exactly these, however, which have the greatest claim upon our interest. They are of the utmost importance to everything which lives and moves on our earth; their formation is the adjustment of one of the greatest contrasts in nature, they form the bridge which connects the inorganic with the organic world, the dead with the living. As a matter of course, these primary organic substances, derived from carbonic acid and water, are the starting-points for all the other chemical compounds of which the bodies of plants and of animals are composed; or, in other words, they form the commencement of all these further chemical changes in living cells which are understood by the term *Metabolism*.

The process of formation of these primary organic compounds is, on the whole, easily comprehensible. It is known that carbon dioxide, *i.e.* carbonic acid, is absorbed by plants, and that oxygen is given out; it is also known that, when this process is carried on in a plant kept in a confined space, a volume of oxygen is given out which is equal to the amount of carbon dioxide taken

up and consumed by the plant. In this way, without doubt, a reduction of the carbon of the carbon dioxide occurs, and hand in hand with this reduction a union of carbon with water must take place. Thus is formed some one of the compounds known as *carbohydrates.* The process has been interpreted in the following manner. The carbonic acid is reduced in the green cells, by the separation of oxygen, to carbon monoxide; this combines with hydrogen to form a body known by the name of formic aldehyde, and from this is produced, by the action of alkaline substances, a carbohydrate. This latter process is more easily understood, from the fact that it has been found possible to produce a sugar from the formic aldehyde (which consists of one atom of carbon, one of oxygen, and two of hydrogen) by means of lime. Thus a definite carbohydrate would be established as the first organic substance formed in a vegetable cell. It is scarcely probable, however, that this carbohydrate alone forms the starting-point for the whole of the other organic compounds in all living plants. It is much more likely that in the large, fundamentally different series of plant-forms, in Fucaceæ, Florideæ, mosses, ferns, conifers, grasses, palms, &c. different carbohydrates are produced as the first organic derivatives of carbon dioxide and water. It must not be forgotten that in this building process the protoplasm of the green tissue plays a very important part, that this is actually the builder, and that the structure and chemical composition of the constructor, or, in other words, the specific constitution of the protoplasm, will not be without influence on the arrangement of the atoms in the carbohydrate formed. The whole of this process has been termed *assimilation,* and by it is meant that the protoplasm in each plant forms materials from the inorganic food absorbed, resembling those of which the protoplasm itself is made up. Assimilating protoplasm thus continues to organize after its own type, and in this matter cannot pass beyond the bounds drawn for it by its own atomic construction. The assumption is now justified that in these formative processes assimilation takes effect from the beginning, and that protoplasm which exhibits a different constitution, and which is known to have the capacity of choosing between the mineral food-salts, will form different carbohydrates. However this may be, this much is certain, that the first organic compound arising in the green cells is a kind of sugar or some other dissolved, undemonstrable carbohydrate.

Under the influence, and by the means of living protoplasm, and in accordance with the requirements of the plant species in question, very diverse alterations and the most varied arrangements and connections, insertions and separations of the atoms are carried on in these primary carbohydrates, and as long as the plant is alive, a continuous transformation of the materials takes place. And this transformation is carried on in very many directions. First, compounds are formed indirectly or directly from the primary carbohydrates. They contribute to the extension of the protoplasm and the envelopes produced from it. Without them no increase in cells, or growth of the plant, would be possible. They may be fitly termed the building materials.

Of the various sorts of building materials, the *albumens* must first be considered; they are to be reckoned as the most important constituents of living protoplasm. Although their chemical composition has not as yet been ascertained with complete certainty, it is known that, besides the carbohydrate constituents, albumens contain nitrogen and 0·8–1·7 per cent of sulphur; that carbon with

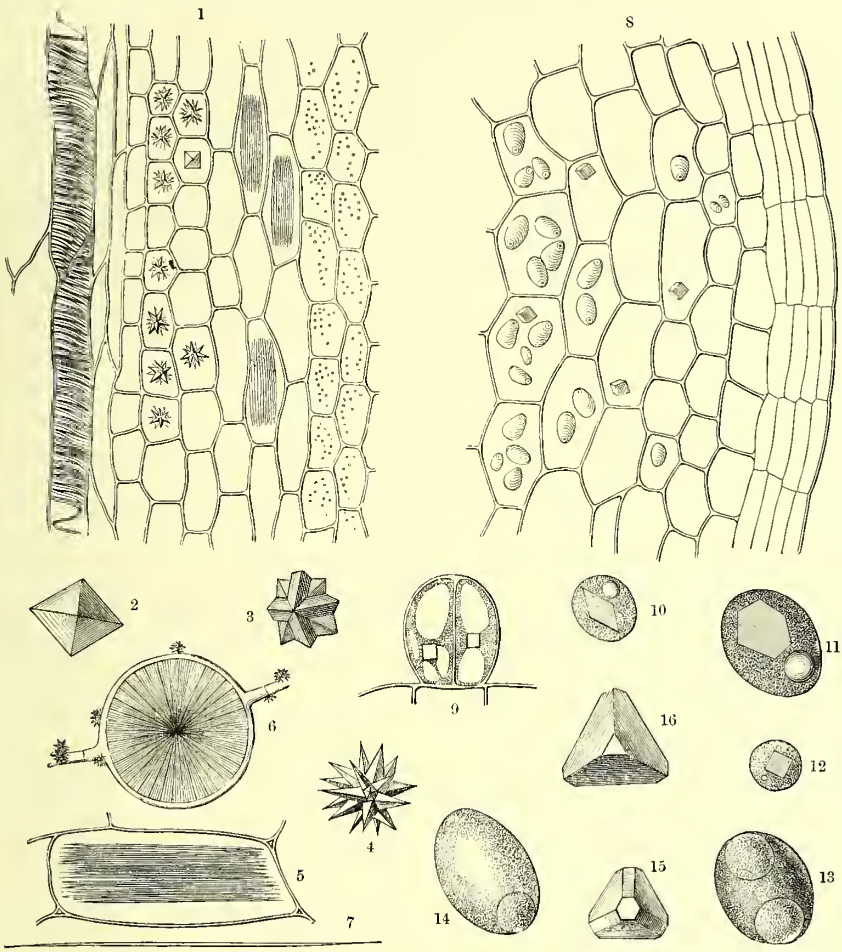


Fig. 123.—Crystals and Crystalloids.

[1] Vertical section through a fallen leaf of the Virginian Creeper (*Ampelopsis hederacea*). In some of the cells are clustered-crystals, in others bundles of needle-shaped crystals (raphides); in one cell there is a single envelope-shaped crystal. [2–5] Solitary and clustered crystals and raphides of oxalate of lime; more highly magnified. [6] Sphere-crystals in the interior of a swollen bladder-like hypha, with small clustered crystals on the outer side of the hyphal thread; from *Phallus caninus.* [7] A single needle from a bundle of raphides. [8] Section of a portion of a Potato-tuber with crystalloids and starch-grains in its cells. [9] Crystalloids in the cells of a gland on a Potato-leaf. [10–12] Crystalloids in aleurone grains. [13, 14] Globoids in aleurone grains [15, 16] Isolated crystalloids. [10–16] From the seed of *Ricinus communis*; very highly magnified.

many, perhaps with more than a hundred, atoms takes part in the construction of a molecule, and that consequently the molecules of albumen are very large. In order that a carbohydrate may become transformed into an albuminous body, nitrogen and sulphur, at any rate, must be drawn into the combination. Nitrogen

is obtained from nitric acid and ammonia, and sundry of their compounds, especially calcium nitrate. These are absorbed by the plant and conveyed by the crude sap to the place of consumption. The nitric acid must, of course, be liberated from this salt, and this is brought about by the union of the calcium with oxalic acid, derived from a portion of the carbohydrates, the two thus forming insoluble crystals and crystalline masses of oxalate of lime (fig. 123). The liberated nitric acid is now reduced in a manner analogous to that of the carbonic acid in the formation of carbohydrates. It is supposed that the nitrogen of the nitric acid then combines with a hydrocarbon, forming an amide (asparagin, leucin, tyrosin), and that the albumen is formed by the union of this with a carbohydrate. Sulphur is derived from the calcium sulphate, or from some other sulphate, by the intervention of oxalic acid, in the same manner as just described for nitrogen. The oxalic acid forms an insoluble salt with the calcium or other base of the sulphate, which separates out in the cells in the form of small crystals. The liberated sulphuric acid must then, in some way, undergo a further reduction, in order that sulphur may enter into the molecule of the albumen. Among the vegetable albumens are to be distinguished albumin, casein, and fibrin. The glutin contained in corn, is a mixture of a casein and a fibrin. All these albumens appear in soluble and insoluble forms. Thus, for example, the conglutin contained in almonds is a soluble casein, and goes into solution when milk of almonds is made by adding water to the almonds; while the legumin contained in peas, beans, lentils, and other pulse seeds, is not soluble in water, and can only be dissolved by pepsin in the presence of an acid. Although all these albuminous compounds cannot be recognized by any definite form, the aleurone grains and the so-called crystalloids have perfectly definite shapes. The crystalloids are formed of albuminous substances, and have exactly the appearance of crystals (fig. 123^{8-12}).

Next to the albuminous substances, the most important building material to be noticed is *cellulose*. This is a carbohydrate consisting of six atoms of carbon, ten of hydrogen, and five of oxygen, and is produced from the primary sugar-like carbohydrates. The transformation is effected by the living protoplasts, which form a layer of cellulose on their periphery, called the cell-wall. At first this cell-wall is mainly composed of pure cellulose; then, according to need, the carbohydrate is changed by the protoplasm, either wholly or partially, into some other carbohydrate, either into woody material (lignin) or cork (suberin), or the cellulose becomes mucilaginous, as, for example, in the seed-coat of the Quince. In the stems and branches of cherry, plum, almond, apricot, and peach trees, the cellulose is generally hardened into a sticky, shapeless, amber-coloured substance, which exudes from the fissures of the bark, and is known by the name of cherry-gum (cerasin). In like manner gum-arabic (arabin) is formed from the cellulose in the stems of some acacias, and gum-tragacanth in several tragacanth shrubs (species of *Astragalus*).

Protoplasm forms cellulose from a portion of the primary sugar-like carbo-

hydrate at certain points in the interior of its substance as well as at its periphery, in addition to another carbohydrate, the so-called granulose. Cellulose and granulose, very intimately intermixed, appear in the form of grains, and the mixture is called *starch* or amylum. Starch-grains are among the commonest of cell-contents. They appear regularly in chlorophyll-bodies and are conveyed from the places where they are first formed to all parts of the plant. This of course is only effected by

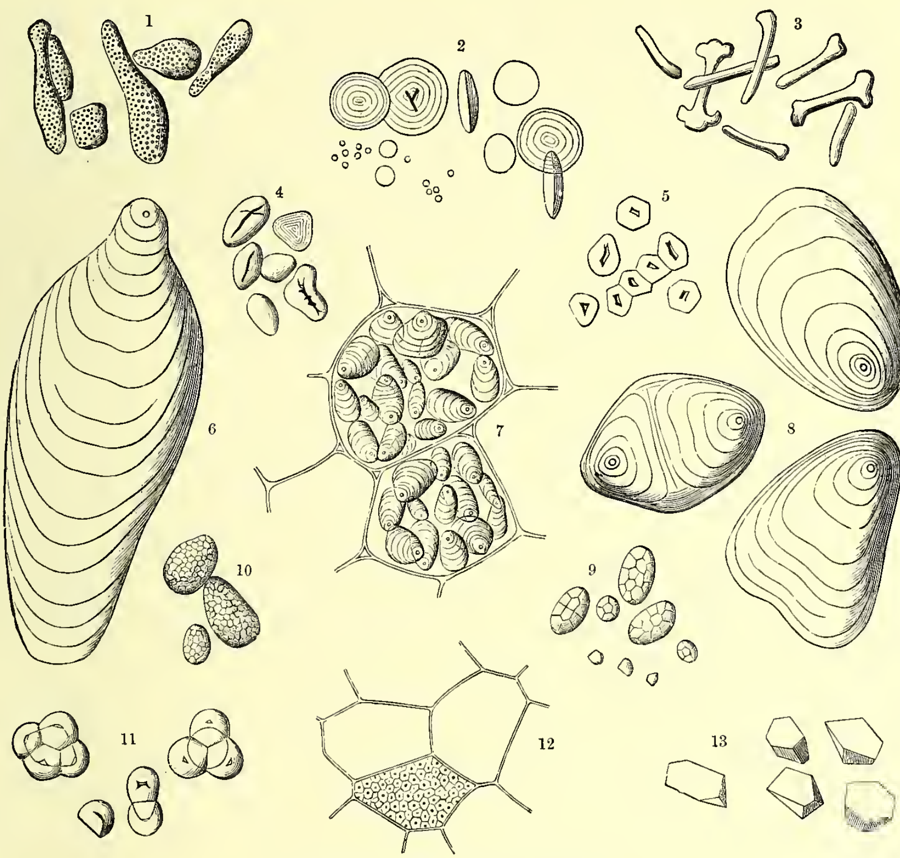


Fig. 124.—Various Forms of Starch-grains.

[1] From the seeds of the Corn-cockle (*Agrostemma Githago*). [2] From a grain of Wheat. [3] From Spurge. [4] From a Bean seed. [5] From a grain of Maize. [6] From the root-stock of *Canna*. [7] From a Potato-tuber (inclosed in cells). [8] From a Potato-tuber (isolated and very highly magnified). [9] From a grain of Oats. [10] From the seed of *Lolium temulentum*. [11] From the corm of the Meadow Saffron (*Colchicum autumnale*). [12] From a grain of Rice. [13] From a grain of Millet. All highly magnified.

the solid starch bodies being made fluid, as often as they pass from one cell to another, by the help of an accessory substance, called *diastase*, which has yet to be described. In many tissues the starch-grains become so accumulated that the cells appear to be crammed with them (see fig. 124 [7]). Starch is one of the most important of reserve materials, *i.e.* of those materials which are not consumed immediately after their formation, but are put away for a time in store-rooms or reservoirs, and then consumed as required in the places needing them. For example, they may

remain in seeds unaltered for years, and as if dead; but if the seed germinates, and the seedling begins to develop, the starch is dissolved, that is to say, becomes changed into another carbohydrate, and finally is made use of in the construction of the cell-walls of the growing seedling by a fresh transformation. Starch-grains in various species of plants differ very much in size as well as in shape. The largest grains exhibit under the microscope alternating blue and red zones, which are accounted for by the difference in the amount of water contained in the several zones. The bluish zones contain less, and the red-tinted more water. Many starch-grains exhibit a "nucleus" or hilum which is rich in water, and which is situated excentrically in the grains of the Potato and of Canna (fig. 124 [6]); centrally in those of the Wheat. A space may be present instead of the hilum, as in the starch-grains of beans and other pulses (fig. 124 [4]), in consequence of the drying up of the substance of the hilum. In most plants the starch-grains have a rounded form; but those of the Corn-cockle (*Agrostemma Githago*) are fusiform and club-shaped (fig. 124 [1]). Those of species of *Euphorbia* resemble tiny bones (fig. 124 [3]), and others again are angular and cornered like crystalline figures (figs. 124 [5] and 124 [13]). This last form is seen especially when the cells which serve as store-houses are densely crowded with starch-grains so that growth becomes checked, and a mutual flattening takes place. In the Oat and Rice many small angular starch-granules are cemented together to form ellipsoidal grains (figs. 124 [9] and 124 [10]), and in the starch from the corm of the Meadow Saffron, regular groups of four rounded grains, each exhibiting a hollow hilum, are found (fig. 124 [11]). Granulose forms the chief of the two carbohydrates which are intimately mixed to form starch. It is soluble in saliva, and is therefore extracted by it, while the cellulose remains behind insoluble, a fact which is of great importance with regard to the digestibility of the starch present in such abundance in flour and bread.

In close connection with these essential building materials are other substances which, though not themselves serving as building materials, take an active part in their production. These furnish the conditions under which the manufacture and transport of the building substances, and the growth and propagation of the plants can occur. They avert injurious influences, regulate light and heat, and are of use to the plant in a hundred minor directions.

To these substances, which may be termed *accessory*, belong, first of all, the *pigments* chlorophyll, phycoërythrin, and anthocyanin, which are so important on account of their relations to light and heat, and whose rôle has already been alluded to. Then we have those compounds whose function is to allure animals to the plants in order to bring about fertilization or the distribution of the seeds and spores, or whose significance lies in the fact that they frighten and ward off animals which might be injurious to the plants. In this connection are of course to be mentioned colouring-matters which are formed in flowers and fruits in order that these may be rendered visible at a distance to those animals whose visits benefit the plant: first of all, anthocyanin, which in the presence of acids is red, but otherwise appears violet or blue; and then anthoxanthin, to which most yellow flowers and

fruits owe their colour. On the other hand must here be mentioned that scarlet-red colouring-matter, as yet little known, probably belonging to the anthracenes and allied to the madder-red, which perhaps serves to frighten animals, and which is so pronounced, for example, in the accrescent calyx surrounding the fruit of the Winter Cherry (*Physalis Alkekengi*).

Besides the colouring-matters, *sweet-tasting substances*, especially cane-sugar, and also mannite and dulcite, play an important rôle of a similar nature. Although their function can only be discussed in detail later on, it is nevertheless well to point out here that the distribution of the spores of Ergot of Rye (*Claviceps purpurea*), for example, is brought about by means of a sweet fluid excreted by the mycelium, which is eagerly sought for by ants and other insects. The insects in sucking and licking up this fluid carry off the spores of the Ergot, and then deposit them on other plants. Countless plants secrete sweet honey in certain parts of their flowers, which serves to attract bees, humble-bees, and butterflies, whose task is to carry the pollen from flower to flower. Certain animals, on the other hand, whose visits would be injurious to the flowers, are kept away, or still better, diverted from them by the honey secreted at the base of the foliage-leaves, which serves as a counter-attraction.

The numerous *ethereal oils*, *resins*, and *balsams* have a like significance for the life of the plant. The ethereal oils are principally hydrocarbons, only a few containing oxygen in addition; oils of lavender, cumin, and eucalyptus, oil of turpentine and camphor, and many others consist of ten atoms of carbon and sixteen of hydrogen. In spite of this similar percentage they differ very markedly in their optical properties, their boiling point, and particularly in their smell, as can indeed be observed from the few examples cited. There are some plants whose foliage, flowers, and fruit contain ethereal oils having different odours, as, for example, the Orange-tree, whose leaves yield "petit grain", the flowers neroli, and the fruit oil of orange. But since these three oils contain the same number of carbon and hydrogen atoms, it must be assumed that their difference depends upon the varying arrangement of the atoms in a molecule. The majority of these oils are transformed into resin by the addition of oxygen, or mixtures of volatile oils and resins are produced, which are called balsams. Volatile ethereal oils, which are perceived by the olfactory nerves even at a distance, function in part as means for alluring animals which benefit the plants in question by transferring the pollen or disseminating the fruits, seeds, or spores; but they also function in part as measures for protecting the plant against attacks from the animal kingdom. The latter is the case especially in foliage-leaves with powerful odours, and in resinous fruits, and these are not used by animals as food. Balsams, which cover foliage-leaves issuing from the buds like a varnish, form a protection against excessive transpiration, and also render material help in the absorption of water by the leaves, as has been already described. The viscous excretions, formed of a mixture of resin and mucilage on the stems and leaf-stalks, which are formed so abundantly in caryophyllaceous plants, keep off animals which try to climb up the stem to reach

the flowers in order to obtain the honey, but which would not be welcome guests to the plant.

Fats take a part in the life of plants similar to that played by ethereal oils. Fats are combinations of fatty acids with glycerine, and may be divided into two groups; in one group the members dry up when exposed to the air by the separation of carbonic acid, as, for example, in poppy oil and linseed oil, which are used for this very reason in oil painting. In the other group, *e.g.* in almond and olive oils, the members remain fluid when exposed to the air, and give rise to malodorous fatty acids, and when this change occurs the body is said to become rancid. The most abundant production of fats takes place in fruits, seeds, and spores, where they are stored up as reserve materials, but in many instances they also function as attractive or protective agents. Nor must we forget the crystalline or amorphous fatty excretions formed on the epidermis of foliage-leaves, stems, and fruits, which are popularly known as "bloom". These are very like wax, and have a very manifold significance; they prevent hurtful moistening by water, regulate transpiration under certain circumstances, and can also ward off the disadvantageous attacks of animals. The branches of many willows which bear honey-laden flower-catkins, as, for example, those of *Salix pruinosa* and *daphnoides*, are provided with these wax-like, extremely smooth and slippery coverings up which the unwelcome wingless ants, scenting the honey in the catkins, in vain try to climb.

Alkaloids and *glucosides* are developed principally as means for protecting the green tissues of the leaves and fruit, and the underground portions of the plants—the roots, rhizomes, tubers, and bulbs—against demolition and extinction by animals. The alkaloids are distinguished by the presence of nitrogen in them. Some of them contain no oxygen, and are volatile, as, for example, trimethylamine, which occurs in the leaves of many oraches, and in the flowers of Hawthorn and Pear, as well as in the American *Pachysandra*. Most, however, are non-volatile, and contain oxygen. To this latter class belong the well-known alkaloids—morphine, nicotine, atropine, and strychnine, which are poisonous to man and most mammals; also the well-known drugs—quinine, cocain, and many others. Leaves provided with these materials are rejected as food by grazing animals, and consequently they at least may be regarded as efficient in protecting the plants from being devoured. Only the volatile trimethylamine in flowers can serve to attract insects. Glucosides, of which more than a hundred are already known, have a use very similar to that of the alkaloids. Saponin is poisonous to man and mammals; amygdalin splits up into the poisonous prussic acid, oil of bitter almonds and sugar; and many others behave in exactly the same way. Tannin has an extremely bitter taste, and therefore protects branches, cortex, and fruits from being eaten. It is interesting to see, that in many fruits which are distributed by means of animals, the pericarp remains acid and unwholesome in consequence of bitter or poisonous glucosides, until the seeds hidden within have matured. As soon as they can germinate, the glucosides become changed; they are split up by means of ferments, which will be described later,

or by the acids which are present in such abundance, into sugar and various other harmless materials, and the pericarp, which, until now had been sharp, acid, and unwholesome, becomes sweet and luscious. The same coat which formerly served as a protection, now forms an attraction. The ripe fruits, with the seeds they inclose, are now sought for and eaten as food, especially by birds; the sweet covering is digested, while the seeds, excellently protected against the action of digestive juices, are excreted with the waste materials of the food, and germinate in the places where they are deposited; thus the widest dissemination of the plants is brought about. All this will be discussed in detail later when distributing agents of plants are being considered; but it seems appropriate to mention these processes here in order to point out that the metabolism of materials in plants keeps pace with the requirements for the time being; that even when the division of labour in the plants is as much developed as in the cases just mentioned, the arrangements and displacements of the atoms, and the decomposition and formation of chemical compounds, are always carried on in the right place and at the right time, *i.e.* always where and when the plant is benefited thereby; and that frequently the reasons for all these changes only become intelligible when we consider the inter-relations of animals and plants.

The significance of salts of sulphuric and nitric acids, as well as the relations of these to oxalic acid, have already been discussed and explained — how by means of the latter the sulphuric and nitric acids are liberated, yielding sulphur and nitrogen for the construction of albuminous substances. If oxalic acid accordingly does not appear to be a necessary plastic constituent of the framework of the plant, it is nevertheless quite indispensable as an accessory to metabolism. The same thing applies to the other *organic acids* which exist in plants. They are only accessories in the transformations, or intermediate steps between the final stages of the compounds formed in the plants, viz. between the first carbohydrate on the one hand, and the completed substance used for building or further purposes on the other. Under these conditions, it is intelligible that the organic acids should be distributed through all parts of the plant, and that the juices in living plants almost universally have an acid reaction. It is also intelligible that the number of organic salts should be extremely large. Oxalic, tartaric, citric, and malic acids may be cited as examples, but more than two hundred such acids are known which have been detected in various plants. Many of them are also found in animal bodies, viz. isolated members of the series of the so-called fatty acids, which form fats when combined with glycerine, as, for example, butyric and formic acids, the latter, as already stated, being also contained in the stinging hairs of nettles. It has, moreover, been already pointed out that glucosides are decomposed by organic acids, and give rise to various kinds of sugar. It is interesting with respect to these sugars that they arise as the first organic products (which result from the assimilation of carbonic acid), and also again as the terminal members of a very long chain of transformations and decompositions of glucosides effected by the action of organic acids. An important

rôle may be assigned to the organic acids of the type of oxalic and formic acids with regard to the turgescence of cells in living plants, since they suck up water with great energy to replace that lost by evaporation, and are thus able to maintain the turgidity.

An especial function is also assigned to the so-called *amides*, by which are understood asparagin, tyrosin, leucin, glutamin, &c. These are produced by the splitting up of albumens, but at the same time they promote the reconstruction of these substances in the living protoplasm. When the carbohydrate, which is derived from the albumen, together with the amide, is used up, the amide again draws to itself a fresh carbohydrate (which has just been formed in the green cells), enters into combination with it, and in this way again forms an albumen. This process may be repeated indefinitely, and will be referred to in the discussion on respiration. Moreover, when albumens, which, in their usual condition, cannot pass through the cell-wall, are to be transmitted from one place to another, they are probably first transformed into asparagin, or a similar amide, which again becomes a complete albuminous compound by the union with a carbohydrate in the place where the albumens are to remain.

Finally, the group of *enzymes* or ferments comes under the head of accessories. These substances, so extremely important to the life of plants, have the remarkable property of being able to decompose other substances without themselves being split up, and in consequence a very small quantity of them can produce very marked results. They all contain nitrogen, and are widely distributed in plants, but since they are only formed in minute quantities in the places where they are required, their presence is not always easy to demonstrate. How they arise is still a problem; perhaps in the same way as the nitrogenous albumens. They are to be found wherever solid bodies are to be liquefied or dissolved; for example, when the stores of organic food, *i.e.* the so-called reserve materials, which have remained resting for a long time in the seeds, tubers, and roots, and have been, so to speak, put out of the way, are to be liquefied and again brought into action; further, when substances which cannot pass through the cell-walls are to be brought into a condition suited to this translation, in which case they act like the amides previously described; further still, as often as organic compounds are to be absorbed as food, insects and other animals to be digested by insectivorous plants, the dead bodies of plants to be broken up by saprophytes, or the organized portions of living plants to be consumed by parasites. When the sucking cells of the parasitic plants wish to obtain the juices of the host-plant; when the hyphæ issuing from the spores make their way through the epidermis into the interior of the plant on which they have fallen; or hyphal threads in the interior of a many-celled tissue wish to pass from one chamber into another, they must dissolve the cell-walls, thus creating an open passage for themselves. Enzymes also appear to come into action wherever those remarkable processes are carried on which are known as fermentations, and which will be considered in the following pages. It is to be supposed that they

form a constituent of the protoplasm of the fermentative organism, and themselves affect and decompose their environment through the cell-wall.

The most important enzymes are, first, *pepsin*, which peptonizes albumens in the presence of weak acids, *i.e.* changing them into a soluble condition, whereby they are enabled to pass through the partition-walls from one cell-chamber to another. The pepsin contained in plants does not, indeed, differ from that in the gastric juice of animals, so that the part performed in both cases is essentially the same. In the stomach of animals it has to perform the important task of bringing the albumens taken in as food into a soluble form, so that they can then enter the blood. The presence of pepsin in insectivorous plants has already been alluded to. Another enzyme to be mentioned is *diastase*, which makes starch grains soluble, since it decomposes them into sugar and dextrin. It is found wherever starch-grains have been stored up when they are again to be utilized and to be assimilated. *Emulsin* and *myrosin* should also be pointed out. They decompose glucosides in the manner already described, and thereby give rise to sweet sugar, especially in fruits; but they can also effect various other decompositions, as, for example, the splitting up of the amygdalin contained in almonds into glucose, prussic acid, and oil of bitter almonds, which is effected by emulsin. *Papain*, occurring in the fruits of *Carica Papaya*, and *invertin*, which has been observed in Yeast, are to be regarded as enzymes. All substances which have a decomposing action on their environment, without at the same time undergoing any chemical change themselves, are called *ferments*, and, so far, all enzymes are to be considered ferments. It has been demonstrated, however, that under certain conditions, acids—for example, phosphoric acid—and even water at a high temperature, exhibit a ferment action, and for this reason the name enzyme has been chosen for the nitrogenous compounds detailed.

We have now enumerated the most important of those substances whose building up and breaking down, whose transformations and interactions constitute what we recognize as the life of plants.

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2. TRANSPORT OF SUBSTANCES IN LIVING PLANTS.

Mechanisms for Conveyance to and fro.—Significance of Anthocyanin in the Transportations and Transformations of Materials.—Autumn Colouring of Foliage.

MECHANISMS FOR CONVEYANCE TO AND FRO.

It has already been explained that the decomposition of carbonic acid, and the formation of organic matter out of the absorbed gaseous and liquid inorganic food, can only occur in cells which contain chlorophyll-bodies. The shape and arrangement of the chlorophyll-corpuscles in individual cells, and further, the form and arrangement of these green cells themselves, have also been there

described. It has, moreover, been stated that numerous plants exist which consist only of single green cells; that others, which are multicellular, exhibit in all their cells the same shape and grouping of the chlorophyll-corpuscles; and finally, that in most seed plants, a division of labour has taken place in each plant, so that certain cells only are provided with chlorophyll, while others are always destitute of it. Many parasites are quite free from chlorophyll, and consequently are unable to decompose carbonic acid and to manufacture organic materials. They are obliged to suck these up from their hosts. Closely connected with these are cases of symbiosis, in which plants possessing, and plants devoid of, chlorophyll enter into partnership, and in which the latter receive in exchange certain freshly-manufactured organic substances from the former. The conclusion of this long series is formed by the saprophytes, devoid of chlorophyll, which derive their organic materials not from living green plants, but from dead animal or vegetable bodies, and from the lifeless organic substances arising out of plants or animals. In the green unicellular plants, as, for example, in the Desmidieæ, two species of which are illustrated in fig. *i*, *k*, Plate I., all the various combinations, arrangements, and separations of the atoms which lead to the formation of sugar, starch, cellulose, chlorophyll, albumen, &c. are accomplished within a single cell; and these minute plants furnish evidence that the manifold changes of the materials connected with growth and construction can occur side by side at the same time and in limited compass. In order to be able to demonstrate this, it must be assumed that each tiny protoplasmic mass, which forms the living body of the single cells, is made up of various portions to which are assigned different functions. One breaks up carbon and forms carbohydrates; another takes up these carbohydrates and forms albumen from them; and yet another transforms the sugar into cellulose and builds up the cell-wall.

With this assumption, however, is necessarily connected the further assumption of a transportation of materials. In unicellular Desmidieæ, the path which the sugar produced in the central chlorophyll-bodies has to travel in order to reach the periphery of the cells, is perhaps only two or three thousandths of a millimetre long; it is, however, a measurable distance, and therefore there is such a thing as conveyance and removal of sugar in cells of Desmidieæ. The transportation is without doubt again carried on by certain portions of the protoplasm, and perhaps the manifold strands which are observed in the substance of the protoplasm are associated with this. In multicellular plants the road which the materials have to follow, in order to reach their destinations, though frequently limited to the space of a single tiny cell, is often represented by a long row of cells. This is especially the case when certain functions are assigned to the different cells of a plant, as happens in many spore-bearing plants, but still oftener in seed-plants. The materials formed in the green leaves of a moss, if they are to be employed in the construction of the spore-capsule and in the production of spores, must be transported from cell to cell, to the archegonium situated on the moss stem—a road which varies according to the species from some millimetres

to several centimetres. The materials which serve to promote the growth of the branches of an Aspen are manufactured in the long-stalked, green leaf-blades of this plant. That they may reach the growing branch, they must pass down the long leaf-stalk and travel along a road many thousand times exceeding the length of those cells in which they were formed. Let us glance at a palm, whose few large leaves, forming a plume, sway about at the summit of a slender stem. In order to reach the growing roots, the constructive materials formed in the green leaves have to travel over a road 20 or 30 metres long. The distance is still greater over which the sap prepared in the foliage of tropical vines is conveyed in order to reach the roots, where it serves as food to parasitic rafflesias growing thereon. It is naturally to be expected that in such instances the routes followed by the travelling materials, and also the starting and end stations, should exhibit characteristic features. What has been ascertained on this point may be here briefly set forth.

The green tissue which is developed in by far the larger number of cases in the cortex of green stem-structures, in foliage-leaves, young fruits, &c., more rarely in floral leaves and roots, must be regarded as the first or departure station. In the green multicellular thallophytes and in mosses, the chlorophyll-containing cells also form the channels of removal for the materials which have been formed in the cells, and these are always extended lengthwise in accordance with the direction of the stream. In the leaves of mosses very frequently cell-rows and cell-bands arise which converge towards the base of the leaf, and in the vicinity of these points the cells are most elongated according to the direction of the current. The conducting cells in the stem are also much elongated in the direction of the current. But here no definite line can be drawn between the forms of the cells at the departure station, in the channel, and at the termination of the current.

It is different in those plants whose leaves and stem are traversed by vascular bundles. These cells devoid of chlorophyll, and peculiar tubes belonging to the bundles, take up the materials proceeding from the green tissues to conduct them to the places of consumption. Division of labour has been so far carried out in all these cases that a portion of the cells undertakes the decomposition of carbonic acid and the formation of the first organic compounds, and another the conveying away of these first products; but obviously this does not preclude the possibility that manifold changes may still take place during the transit. In such a division of labour it is important that the organic compounds which have been formed in the superficial green cells, under the influence of light, should be removed as quickly as possible from the places where they are produced, so that the important process of the decomposition of carbonic acid should suffer no kind of interruption. It is on account of this rapid removal by the shortest path that the green cells are elongated in the direction in which they transport their products, and that the neighbouring green cells are separated as much as possible from one another. However they may be arranged in other respects, the indicated direction and isolation are always observed by them under all circumstances.

The isolation is brought about by the elongated cells, which lie parallel side by side, assuming a cylindrical form in consequence of which they merely touch one another, leaving large air-spaces between. An exchange of materials between these cylindrical cells, *i.e.* a passage of materials transversely across their elongated sides is wholly prevented, and the transport of the materials is effected only in that direction in which the cylindrical cell in question is elongated. The organs which convey the materials away from the green cells lie within the strands which form the veining of the leaf, which traverse the leaf-stalk and stem as thick bundles, and when densely aggregated, form the chief part of the trunks of woody plants. But it would be erroneous to suppose that these strands (*i.e.* the vascular bundles) are composed exclusively of structures for conveying away plastic materials. Adjoining these, and connected with them, are regularly found woody cells, tubes, and other vessels, which conduct the mineral food-substances absorbed by the roots, and the water in which these are dissolved, upwards to the transpiring tissues. Finally, elastic thread-like bast-cells are always added to these structures, which serve for the two kinds of transport, by which means the whole is given the necessary firmness and elasticity. In these strands, therefore, which are called vascular bundles, the most varied structures with widely-differing functions are found crowded together in a small space, and it happens that the cells and vessels which serve as the passage for the current of organic materials formed in the green tissues, only occupy a very moderate share of the space.

Four kinds of mechanisms for carrying on the work of removal have been discovered. First of all, there are groups of parenchymatous cells which adjoin the other elements of the vascular bundle, especially the water-conducting woody cells and vessels which they usually surround, forming an actual mantle round them, termed the *vascular bundle sheath.* These vascular bundle sheaths are particularly well developed in the foliage-leaves, and form there an important constituent of the leaf-ribs and veins traversing the green tissue (see fig. 126 [2]). In the finest and most delicate veinlets, representing the ultimate terminations of the vascular bundles, the few water-conducting cells, stiffened by spiral thickenings, are surrounded by parenchymatous cells. These are continued on beyond the vascular bundle, and frequently the finest veinlets are formed to such a large extent of these parenchymatous cells that they have been distinguished as a particular form of tissue by the name of nerve-parenchyma.

Next to the vascular bundle sheaths, medullary rays are to be regarded as organs for conveying the formed materials from the green leaves. These consist also of parenchymatous cells with lignified walls which are elongated at right angles to the axis of the stem-structure to which they belong. They form layers of tissue which are situated between the vascular bundles, and connect the pith in the centre of the stem with the cortex. Besides these medullary rays, which are known as primary, quite similar layers are formed of parenchymatous cells in the body of the vascular bundles, which, however, are in no way connected with the pith in the centre of the stem, and which are known as secondary medullary rays. On cutting

across the trunk of a fir or of a leafy tree, it is seen that in most cases the vascular bundles in the cross section are so arranged that they form together a ring round the central pith. This ring appears interrupted by the tissues just described, which radiate out from the medulla; and thus is explained their name, medullary rays.

Soft bast is to be considered as a third form of conducting mechanism for the organic compounds formed in the green cells. It consists partly of thin-walled parenchymatous cells, and frequently also of long, narrow cells tapering at the ends (cambiform cells), which are elongated in the direction of the bundle or strand to

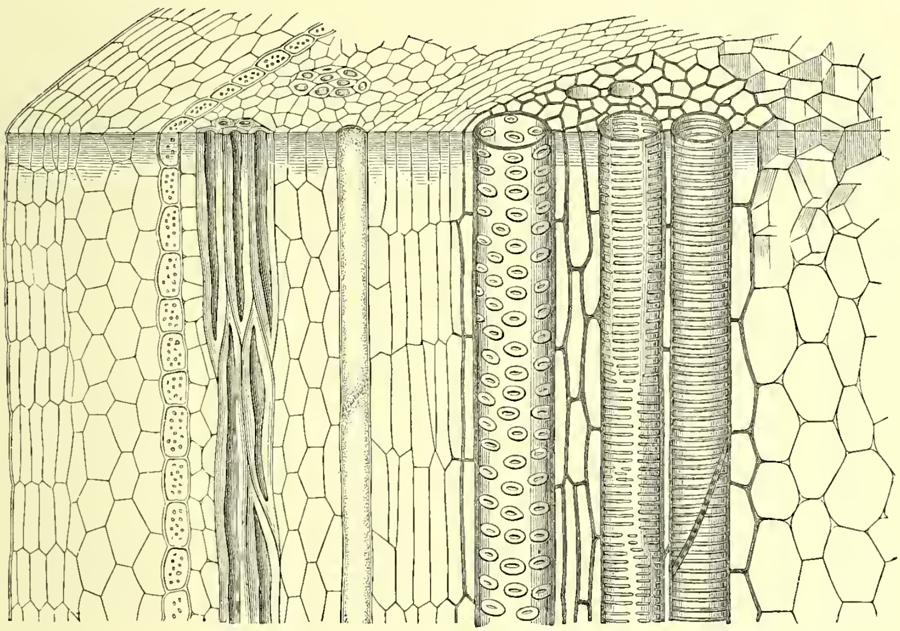

Fig. 125.—Portion cut from a Branch of a Leafy Tree; × about 200. Diagrammatic.

[1] Superficial coat (Epidermis). [2] Cork (Periderm). [3] Cortical parenchyma. [4] Vascular bundle sheath. [5] Hard bast. [6] Bast parenchyma. [7] Sieve-tubes. [8] Cambium. [9] Pitted vessel. [10] Wood-parenchyma. [11] Scalariform vessels. [12] Medullary sheath. [13] Medulla or pith.

which they belong, and form a tissue called the bast parenchyma (see fig. 125 [6]). The other part of it consists of tubes which contain walls separated by comparatively large intervals, often measuring 2 mm., usually placed horizontally, but often obliquely, which give the tubes a jointed appearance. Sharply-defined perforated areas appear on the interpolated horizontal walls as well as on the lateral walls of the tubes, they have a sieve-like aspect, and are called sieve plates, the tubes themselves being called sieve-tubes, bast-tubes, or bast-vessels (fig. 125 [7]). The soft bast but rarely forms isolated strands, as, for example, in some Melastomaceæ; as a rule, strands of firm, elastic, string-like, hard bast cells adjoin it, but these have nothing to do with the transportation of materials, and have merely a mechanical significance (see fig. 125 [5]).

This fibrous or hard bast, together with the soft bast, forms in very many plants

one-half of the vascular bundles, the so-called bast portion, while the other half, the so-called woody portion, consists of woody cells intermingled with lignified tubes, and other water-conducting elements (see figs. 125 [9, 10, 11]).

Laticiferous tubes form a fourth mechanism for conducting away the products of the green cells (fig. 126 [1]). These are thin-walled, much branched, frequently anastomizing, tubular structures which seem to penetrate all the parts of the plant, leaves, stem, and roots, without much regularity.

They may be divided, according to their development, into laticiferous vessels and laticiferous cells. The former are produced from rows of cells, whose partition-walls have become obliterated, so that the rows of cells have become converted into tubes; the latter arise from isolated cells, at first very small, but which elongate enormously, become much branched, and whose branches penetrate between the cells of other tissues just as the hyphæ of parasitic fungi grow through the tissues of their host-plants. Laticiferous tubes are not to be found in all plants. They are particularly abundant in species of Spurge, some thousand species of Compositæ, for example, in the Salsify, Lettuce, and Dandelion; in the Oleander, many Asclepiadeæ, Papaveraceæ, and Artocarpeæ. In the gigantic trunks of tropical Fig-trees, the latex often wells up in large quantities from rifts in the bark which have arisen spontaneously, and thickens into long strings and ropes of india-rubber hanging down like a mantle.

The Cow Tree of Venezuela (*Galactodendron utile*) is especially worth noticing here; when pierced, a quantity of sweet, delicious milk pours out from it, also *Collophora utilis* of the Amazon, from which is obtained a viscous latex, used as a medium for colouring matters; finally the poppy (*Papaver somniferum*), whose dried latex is known as opium. In the majority of cases the latex is white, but in Papaveraceæ other colours are also to be found; thus the Celandine (*Chelidonium majus*) contains an orange, and the Bloodwort (*Sanguinaria Canadensis*) a blood-red latex. The milky Agarics (*Lactarius*) contain partly white, partly sulphur-yellow, partly orange, and vermilion latex.

In the foliage-leaves the laticiferous tubes run with the vascular bundles, and occasionally replace the bundle sheath; at least, the bundle sheath is defective, and only very incompletely formed where the laticiferous tubes adjoin the vascular bundle. It has also been observed that in the stems of the Asclepiadeæ, where the laticiferous tubes are abundantly developed, the sieve-tubes are much reduced, and it is therefore supposed that the various mechanisms for conducting away materials are sometimes able to mutually replace one another. It must, moreover, be expressly noted here, that the laticiferous tubes do not serve exclusively to carry away the materials manufactured in the green cells; they are used, under certain conditions, and at certain times, as receptacles for reserve materials, exactly as the medullary rays, sieve-tubes, and bundle sheaths which in the winter, when the decomposition of carbonic acid, and the formation of carbohydrates in the green cells have ceased, and when generally there is nothing to remove, function as reservoirs, in which stores are deposited until the following spring. The parenchy-

matous cells of the vascular bundle sheaths which, in summer, had been used for conducting away materials, are then crowded with starch-granules, the pores of the sieve-plates are closed up during the winter; the sieve-tubes, laticiferous tubes, bundle sheaths, and medullary rays do not again commence their activity until the next period of vegetation, when everything becomes liquefied, and the green cells again form fresh carbohydrates. These structures then serve again, of course, chiefly as conducting organs.

With regard to the junction of the conducting organs with the green cells, we have a very great variety, but the many different contrivances may be grouped into

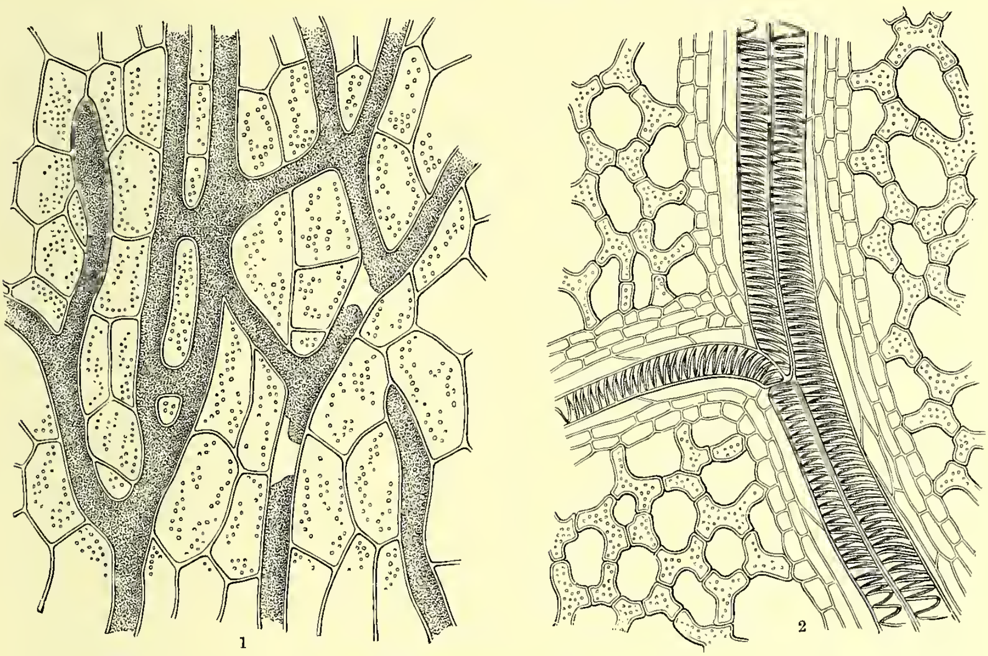

Fig. 126.—Organs for Removal of Substances.

1 Laticiferous tubes from the leaf of *Lactuca virosa*; × 250. 2 Vessels with spirally thickened walls, surrounded by the bundle sheath, from a leaf of *Ricinus communis*; × 210.

two chief forms, viz. where the junction is direct, and where it is effected by means of specially interpolated cells.

In the first group, the switch shrubs are first to be noted, in which the foliage is entirely or almost entirely absent, and where the main portion of the green tissue is developed in the cortex of the rod-shaped branches, as, for example, in *Cytisus radiatus* and in the Broom (see figs. 69 3, 69 4, 81 1, and 81 2). Here the ring of vascular bundles forming the framework of the whole branch is surrounded by a common bundle sheath, and the cells of the green tissue in the cortex are connected on one side with the epidermis, and on the other with this bundle sheath, to which the organic materials produced are given up directly. In the foliage-leaves of many liliaceous plants, especially in the equitant leaves of irises, the green cells are elongated transversely, forming a kind of bridge stretched between the vascular

bundles, which run almost parallel from the base to the apex of the leaf. Each of the bridge-like green cells is connected at either end with a vascular bundle, and delivers the materials produced to the conducting portions of these vascular bundles on both sides, *i.e.* to the vascular bundle sheaths. In other liliaceous plants, especially in the leaves and green stems of species of onion, the green cells are palisade-shaped, and their longer diameter is perpendicular to the surface of the part to which they belong. Here we have only a one-sided connection with the conducting cells of the vascular bundle, but the junction is again a direct one. Finally, the peculiar connection of laticiferous tubes with the palisade-cells in the leaves of species of spurge must be considered.

Although the laticiferous tubes appear to be very much branched wherever they occur in plants, the formation of branching tubes is nowhere else so abundant as in the vicinity of the palisade-cells. Many of the twigs directly adjoin these cells. It also happens that single terminations of the laticiferous tubes impinge upon the lower ends of several palisade-cells, which are inclined towards one another (fig. *s*, Plate I.), and that single laticiferous ramules push their way in between these cells. In all these examples the materials manufactured in the green tissue are taken up without further intervention by the ultimate terminations of the conducting laticiferous tubes.

Of the second group, which is characterized by the fact that the junction is brought about by specially intercalated cells, the first instance to be considered is that often observed in the leaves of grass-like plants, where the intermediate cells, which are also called conducting cells, are more or less extended transversely, and unbranched. The green cells lying under the epidermis are palisade-shaped, and at right angles to the leaf-surface; the longer diameters of the cells lying below these, which are much poorer in chlorophyll-corpuscles, are, on the other hand, placed obliquely to the leaf-surface, or even parallel to it, and apparently are directed towards the large cells of the bundle sheaths in the middle of the leaf. These cells, poor in chlorophyll, therefore connect the palisade-cells with the conducting cells of the bundle sheath, and serve as agents in the removal of the substances. But the commonest cases are those in which the conducting cells are much branched. The foliage-leaves which possess these branched cells are differently constructed on the upper and under sides of the leaf. Under the epidermis of the upper side is seen the palisade-tissue, consisting of cylindrical or prismatic cells, whose long axis is directed perpendicularly to the plane of the leaf (see fig. 62 [1] and Plate I. fig. *r*). Below these palisade-cells come the branched cells, which are connected with one another by their arm-like processes, forming a large-meshed tissue, the frequently-mentioned spongy parenchyma, interrupted by wide interstices. The spongy parenchyma is connected with the palisade-tissue by means of single processes bordering the lower, that is to say, the inner ends of the palisade-cells; very often a single process is connected with the inner ends of several palisade-cells, in which case these have a clustered arrangement. As with the palisade-cells, the branched cells of the spongy parenchyma are connected with

the parenchyma sheaths of the veins. Thus the branched cells of the spongy parenchyma become agents in the transportation of the materials; with one branch they take up the organic substances manufactured in the palisade-cells, and with another they deliver these materials up to the bundle sheath for further translation to the places of consumption or storage.

That the cells of the spongy parenchyma serve not only for conduction, but have to perform several other functions, does not need to be confirmed in detail. It is enough to point out that they contain chlorophyll-corpuscles, and therefore are capable of decomposing carbonic acid and of forming carbohydrates, although to a much less extent than the palisade-cells, which are so richly supplied with chlorophyll. Moreover, the excretion of aqueous vapour occurs in the spongy parenchyma whose lacunæ and passages communicate with the outer world by the stomata, and where also a vigorous inflow and outpouring of other gases takes place. Then the part which the conducting structures play in the metabolism of the materials must not be overlooked. All these structures contain active living protoplasm, in all there is a protoplasmic cell-body, although very often it is only in the form of a delicate parietal layer, and in all, under the influence of this living protoplasm, we have not merely a movement, but also an inexhaustible and infinite changing of the materials, corresponding to the individuality of the species and to the requirements of the time being. These structures must then be regarded not only as simple channels for the fresh carbohydrates produced in the green cells, but also as regions for transformations, where the first organic compounds manufactured in the green cells are prepared for ultimate consumption at the end of the journey. It is precisely in this respect that they differ essentially from that conducting apparatus, whose task is to transmit water and mineral salts to the green tissues, and which, as already repeatedly remarked, is present in the same bundle as the cells and vessels which take away the organic materials. When once the water-conducting tubes and cells have attained their full dimensions, they no longer contain protoplasm, and no transformation of the transmitted raw food-sap is carried on in them; the water, with the mineral food-salts dissolved in it, is carried through them unaltered to the transpiring cells. To employ the simile, often used before, of the arrangements of a well-conducted household, the woody cells and vessels of a vascular bundle may be compared to an apparatus for delivering water and salts into the kitchen, so to speak; the green tissue forms the kitchen in which the raw materials are worked up and so prepared that they can be brought back by the removing cells to the places where they are required and consumed.

That these two fundamentally different kinds of conducting apparatus are so universally found united together in one and the same bundle is explained by the fact that the places which form the goal for one are at any rate to some extent the starting-point of the other; besides, of course, this combination economizes the building materials. All conducting apparatuses must be strengthened and protected in their position, and therefore it is beneficial and saves building materials if

the different structures taking part in the conduction are mutually of use to one another, and are protected and saved from injurious external influences by the same arrangement.

The vessels and cells whose task is to conduct water and salts become lignified, and the massive bodies of wood which exist in the trunks of old woody plants form such a firm support that the thin-walled soft bast, when it clings to these and runs parallel with them, is excellently protected from breaking. In those organs which require to resist bending, however—in leaf-ribs and leaf-stalks, culms, and young branches,—hard bast is put in as an accompaniment of the cells and tubes which conduct up and down. These strands of thick-walled, but at the same time flexible and elastic, cells of hard bast prevent the organs which they adjoin from being broken and ruptured even under the influence of a considerable push and strain. Let us look at the haulms, stems, branches, and leaves in a meadow or in a wood during the sultry period which precedes the outburst of a storm. Not a leaflet stirs, even the supple haulms are still, and every part of the plant, that true child of light, assumes that position with regard to the light most beneficial to it. The storm bursts, the wind whistles over the meadows, the leaves tremble, sway, and flutter, the leaf-stalks shake, the culms bow and bend, the stems and branches are smitten and arched so that their tops almost touch the ground; the foliage is pelted with the rain, and shaken and displaced by every drop that falls on it. An hour later the storm is over; here and there perhaps may be still seen a group of stems and leaves prostrate under the weight of the rain-drops, and part of some herbaceous stem which has been shaken by the storm bent like a bow, but the rest stand again erect and motionless, as if they had never been disturbed by a breeze; finally, even the plants bent by the shock and so severely prostrated by the rain-drops raise their branches and foliage, and everything again resumes the same conditions and position as before the outbreak of the tempest. But this is only rendered possible by the presence everywhere of the elastic flexible strands of hard bast accompanying the sieve-tubes and the other soft and delicate structures which take part in the preparation and transportation of the organic materials. It is indeed unavoidable that the cross section of the cells and vessels should become narrowed in consequence of the push and strain caused by the gusts of wind, and that, for example, the cross section of a cylindrical tube should become elliptical in consequence of the curvature; but since the prostrated stem or leaf again rebounds into the former position by reason of the elasticity of the hard bast, the alteration produced by the push and strain is only temporary, necessitates no interruption of function, is perhaps even beneficial to the movement of the materials, and, which is the main point, no rupturing and no permanent bending of the soft delicate-walled structures ensues.

These delicate-walled elements, especially those of the soft bast, are protected against harm from lateral pressure by the deposition of various tissues, especially cork, in front of them (fig. 125 [2]), which, like the buffers of an engine, keep off, or considerably weaken, the lateral thrust and pressure. Remarkable contrivances for

protection against lateral pressure are also found in creepers and climbing plants with perennial woody stems, and in those plants which are commonly called *lianes.* In order to comprehend these contrivances rightly, it is necessary first to get an idea of the position of the parts requiring protection in perennial woody plants,

Fig. 127.—*Rhynchosia phaseoloides*, a Liane with ribbon-like Stems.

which neither climb nor creep, and which possess an erect, straight, column-like trunk. As previously stated, in these plants to which belong the firs, oaks, beeches, elms, limes, apple-trees, and, generally, the majority of leafy trees, the vascular bundles are arranged in a ring round the central pith, and consist essentially of the woody portion, serving to conduct the raw sap, and the bast portion, which is employed in the transmission and transformations of the organic substances formed in the green cells. These two portions are separated in the plants men-

tioned by a layer of tissue in which a very vigorous formation of new cells is carried on, termed the *cambium* (fig. 125 [8]). From this cambium, which appears as a ring in the circular cross section of erect stems, cells develop which on one side abut upon the wood already present in the interior, and on the other the existing bast portion of the vascular bundle to the exterior. In this way both portions, and in fact the whole stem, increase in dimensions; and in the wood, in particular, arise the *annual rings* which are visible in a cross section. The cambium ring also stretches; it becomes larger and larger, but always retains the same position and relation to the wood and bast of the vascular bundle, and keeps its ring-like form although the trunk in question may have become ever so old and thick, and may exhibit hundreds of annual rings. Here, therefore, the soft bast lies outside the cambium ring, and is screened towards the exterior by various tissues, by hard bast and corky tissue among others, and the latter may undergo considerable development in trunks of many years' growth; while the hard bast, on the contrary, diminishes in older trunks, because it is no longer required as a protection against bending. Accordingly the soft bast is situated fairly near the surface. Since a strong external lateral pressure is not to be feared in them, this position cannot be characterized as unfavourable. The cork and other external portions of the cortex comprehended under the term *bark* afford a sufficient protection against small pressures in old stems. In lianes it is very different, especially in those which make use of erect stems as supports. Apparatus for increasing the bearing capacity and elasticity in lianes would be superfluous, these tasks being performed by the support; on the other hand, a protection against lateral pressure is urgently required, for if the support up which the lianes climb, to which they are attached by adventitious roots, or which they encircle and entwine, increases in thickness, as is usually the case, then a lateral pressure on the adherent liane coils is unavoidable. And when, as a result of such pressure, the sieve-tubes and bast parenchyma become squashed over considerable distances, they are obviously unable to perform their functions satisfactorily, and nutrition will certainly be impaired. Lianes are protected by the most varied contrivances against this source of injury, and some of the most striking will be here briefly indicated.

In *Rhynchosia phaseoloides*, the young, green, twining stem is circular in cross section, and exhibits a structure which does not differ materially from that of young normal stems. In the centre is a pith, round which the vascular bundles form a ring—first wood, then soft bast, further out hard bast, then a layer of green cells, and, finally, the epidermis, which envelops the whole. It might be expected that in the second year, the newly-formed cells and tubes would deposit wood on wood and soft bast on soft bast, and that the cylindrical stem would increase regularly in circumference without altering its shape. But, strangely enough, this does not happen. New cambiums arise at two points near the periphery of the stem, below the green cells, by which the formation of wood proceeds in the direction of the first year's vascular bundle ring (*i.e.* inside), and soft bast accompanied by hard bast on the opposite side (*i.e.* outside). At

the end of the second year the stem is no longer circular, as at the first; it has added two rings, as it were, and now appears elliptical in cross section; and since new portions are added in this way repeatedly from year to year, and new rings are always becoming annexed to those already existing, the stem gradually becomes ribbon-like, and exhibits a cross section like that shown in fig. 128 [2]. The soft bast has thus received the most protected position imaginable, and lateral pressure is unable to interfere with its functions. When the supporting stem round which the *Rhynchosia* has twined grows enormously in thickness, the liane becomes stretched, and experiences a lateral strain, but the sap can, nevertheless, continue its journeys unhindered in the soft bast.

In the liane *Thunbergia laurifolia*, a cross section of whose stem is represented in fig. 128 [1], the protection is obtained in quite a different way. Here the green

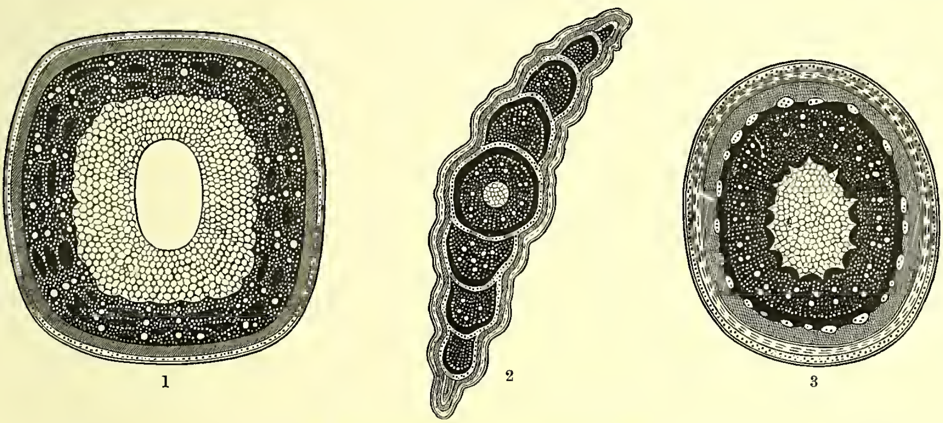

Fig. 128.—Transverse sections of Liane Stems.

[1] *Thunbergia laurifolia.* [2] *Rhynchosia phaseoloides.* [3] *Tecoma radicans*; × 30. Diagrammatic. The various tissues are indicated in the following manner: Soft bast, entirely black; wood, larger and smaller white dots on a black ground; hard bast and other mechanical tissues, obliquely shaded; cork (*periderm*), short lines; pith, reticulated.

stem is hollow, and the cavity is surrounded by an enormous pith. In the vascular bundle ring which surrounds the pith, the wood and hard bast are not arranged from the first in successive concentric circles, as is usually the case, but are placed side by side. The cambium continues to form soft bast in some places, and wood in others, towards the interior. In consequence of this, the bundles of soft bast appear to be walled in by the wood ("bast-islands"), and are consequently well protected against pressure. The protection is increased by the fact that this liane is hollow in the centre, and can "give", an uncommon feature in twining plants.

Sometimes the delicate soft bast is protected against compression by its position in niches and grooves at the periphery of the hard wood; this is to be seen especially in several twining Asclepiadeæ and Apocynaceæ. One of the most remarkable protective arrangements is found in the climbing *Tecoma radicans*, which adheres to its substratum by tufts of aërial roots, and whose leafless branches are depicted in fig. 129. A cross section of the stem is shown

in fig. 128 [3]. The young branches rooted to the wall are elliptical in transverse section, being always somewhat compressed on two sides. The outer portion is composed of the epidermis, two layers of elastic parenchymatous cells below it, and a layer of green cells. Then comes the ring of soft bast, outside which bundles of hard bast are deposited; then the rings of cambium and wood, and in the centre a large pith, which sends out single- and double-rowed medullary rays through the wood ring. So far the arrangement of the various tissues exhibits nothing particularly noticeable, and coincides with that in the young branches of numerous woody plants. But tracts of cambium cells are subsequently formed in a remarkable manner on the inner side of the ring of wood adjoining the pith; these develop wood towards the exterior and soft bast on the interior. The constituents of the soft bast—sieve-tubes and bast parenchyma—form quite conspicuous bundles which project into the pith, and being here excellently protected against lateral pressure, can perform their duties undisturbed. Should the conducting cells and sieve-tubes of the outer ring of bast not perform their duty, these inner ones still remain for the transmission of the plastic materials.

Thus the various arrangements of the constituents of the stem, and especially the position of the channels for the streams of materials formed in the green tissues, is in part accounted for by the protection gained against the injurious action of external pressures and strains, and these act in the most varied way on the exterior, according to the individual mode of life of the plant and the conditions of its habitat.

It is to the growing parts of plants, the extremities of roots and branches especially, that organic matter is conveyed; also to places where the cells already present become stimulated to fresh activity, where dead and dying cells are replaced by fresh ones, and where constructive materials in sufficient quantity must be at hand. Then again, the travelling substances are directed to those places where protective and attractive agents are necessary to contribute indirectly to the maintenance and multiplication of the species, and where a consumption of materials is connected with this protection or allurement. It is thus of importance, for example, that the honey excreted from certain parts of flowers, which serves as food to the insect guests which effect fertilization, should be always present in sufficient quantity, and that in case of its removal from the receptacles by bees or butterflies, it should be immediately replaced by fresh supplies. Care must also be taken that pepsin and other substances necessary for digesting prey should be abundantly present in the pitfalls and other mechanisms which serve for the capture of animals, and that a sufficient quantity of alkaloids and bitter substances, which prevent ruminants from devouring foliage, should be brought to the right places at the right time. In connection with the process of rejuvenescence and multiplication also, it is necessary that those cells and groups of cells, which become detached from the plant-shoot and journey out into the wide world as spores and seeds, should be equipped with

a store of materials, so that they may be nourished until they can manufacture for themselves the necessary food from the air, water, and soil. The places where spores and seeds are produced, therefore, constitute an important destination for certain journeying materials. Finally, it also happens that in regions where a temporary standstill of the vital activity of the plants occurs, and where the succulent green foliage is liable to be dried up by the periodic drought, or frozen by the winter cold, all the useful substances are withdrawn from the threatened

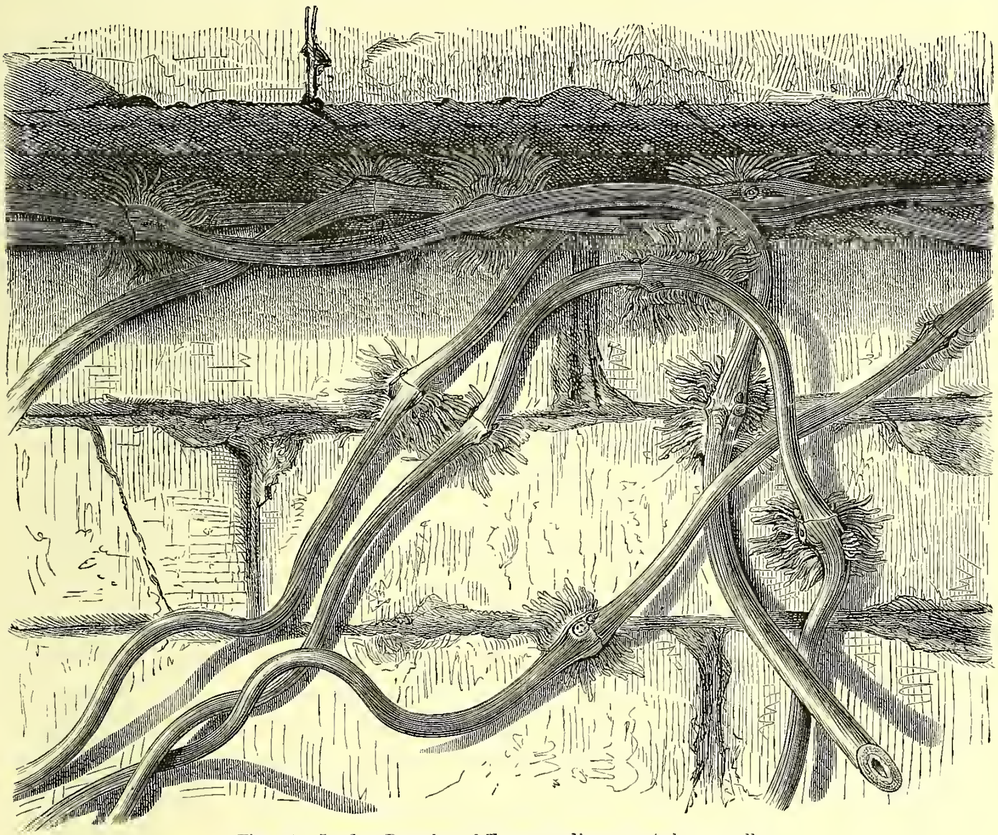

Fig. 129.—Leafless Branches of *Tecoma radicans*, rooted on a wall.

leaves, and are deposited in a suitable form in safe places, and stored up for employment later. In these instances, these safe places, these storehouses or reservoirs, form the destination of the transported materials.

Not only are there channels of distribution to the various destinations enumerated, but we find even distinct routes provided for the different substances transmitted. Investigations have shown that the conducting mechanisms divide the work to some extent between them. The medullary rays and wood parenchyma chiefly conduct carbohydrates, the former radially, and the latter longitudinally, in the stem. The vascular bundle sheaths of the leaf-veins are particularly rich in glucosides. Certain tracts of cells in the parenchyma accompanying the vascular bundles in the stem also conduct glucosides, while others conduct sugars

(sugar sheaths), and others again are the route for the transmitted starch (starch sheaths). The sieve-tubes and bast parenchyma, on the other hand, convey principally albuminous substances which are employed as constructive materials for the growing and enlarging portions of the plant.

This important relation of the soft bast to the growing organs explains many remarkable phenomena, two of which must be briefly described here. First, the surprising increase of growth in certain places which gardeners produce by the operation of *ringing*. If two parallel circular cuts are made round a growing branch of a tree through the whole thickness of cortex down to the wood, and if the circular piece of cortex, together with the soft bast lying between the two cuts is removed, the sap current in the soft bast from the upper portions to the base of the branch is interrupted. The cut surfaces dry up; the route down the soft bast is therefore closed, and the part of the branch lying below the excision can no longer receive from the soft bast the materials necessary to its further growth. The same result is obtained by passing a cord tightly round the young leafy branch of a tree at some spot, say about half-way up. In this way all the soft tissues which lie outside the wood, including the soft bast, are compressed, the sieve-tubes and tracts of cells of the bast parenchyma tightly squeezed together, and the conduction of sap by them to the base is rendered impossible by the strangling cord. The ascending current of water and dissolved food-salts, in the deeper-lying firm wood, flows on unimpeded in either case. The green foliage-leaves can thus decompose carbonic acid and manufacture organic substances above the circular cut or ligature; these products are then conducted away; the albuminous substances enter the soft bast, but only travel as far as the place where the cut has been made or the ligature been tied. They can no longer pass these places, and consequently the plastic albuminous materials become dammed up above the "ring" or ligature, and a particularly luxuriant growth of all these parts results. Fruits which develop from the blocked-up region of the branch sometimes enlarge to an extraordinary degree, and become almost twice as heavy as they would have done had the operation not been performed.

The following phenomenon is also explained by the fact that the passage of plastic albumins takes place in the soft bast. If a branch of a willow, *e.g.* of *Salix purpurea*, be cut off and the entire cortex down to the wood be removed from the lower third of the branch, and the branch so treated be then plunged half-way into a vessel of water, after a time it will send out roots into the water. But these differ from one another very much according as to whether they arise from the lower stripped portion of the branch or from higher up where the cortex has not been removed. The roots developed from the stripped portion are few and remain very short; those springing from the upper thickening portion of the willow branch, where the cortex is intact, are, on the contrary, abundant and elongated, since they can utilize the plastic juices above the place where the cortex, together with the soft bast, has been removed.

Both of the experiments described only exhibit the results mentioned when performed on plants, the whole of whose soft bast bundles lie outside the cambium ring, since interruption of the sap-current by ringing only takes place under these conditions. If plants are experimented on which possess internal bundles of soft bast in addition to those lying near the surface, as in *Tecoma*, *Thunbergia*, and many others, the ringing does not have the result described, because the inner bundles of soft bast (being protected by the hard wood) are not cut through by the knife, and cannot be compressed by the ligature. It should, however, be observed that even in woody plants, whose soft bast lies entirely outside the cambium ring, this result is restricted to the year in which the ringing or ligaturing was performed. In consequence of the absence of supplies of albuminous materials through the soft bast, the portion of the branch below the cutting or ligature becomes unhealthy, its cortex dries up and dies, and the disparity between the two portions lying above and below the ringed cut or the tight ligature usually occasions the death of the whole branch tampered with in the following year.

In the tubular conducting mechanisms, especially in the laticiferous tubes, which are entirely free from transverse walls, and also in sieve-tubes, in which perforated horizontal walls are inserted here and there, a transport of substances *en masse* may occur, but this is impossible in those conducting apparatuses consisting of rows of cells whose length is usually only three or four times their width. In these tracts of cells the numerous non-perforated partition-walls of the adjoining cell-chambers are interposed, and must be passed through by the travelling materials. Whether this passage through the walls be regarded as a diosmosis or a filtration, it is at least certain that solid bodies of definite form cannot traverse the walls. Even starch-grains of the smallest diameter are always much larger than the interstices which we imagine to exist in every cell-wall between the groups of molecules; and therefore it follows that even the tiniest visible bodies must always remain behind, as on a filter, in one of the two adjoining cell-chambers, that is to say, on one side or the other of the dividing partition-wall. Accordingly, only fluid materials travel through such cell-tracts as serve for the conduction of substances in the soft bast, parenchyma, and in the bundle sheath. If solid substances take these routes, they must be first brought into a soluble condition. This applies especially to the starch-grains which play such an important part in the life of plants, and not only share in the formation of cellulose, chlorophyll-corpuscles, and fats, but are also heaped up in the storehouses of the plants as materials well suited for storage during the summer drought or through the winter, for use in the next period of vegetation. They are also given to the seeds which have to lead an independent existence, as the first food for the journey after leaving the parent plant. If starch-granules are to travel through the cells of the bundle sheath, composed of hundreds of single cells, they must be dissolved a hundred times, and a hundred times reformed. It has been definitely proved that this *transitory* starch is not liquefied at the beginning of its journey and again formed into solid only when it has reached its destination, but that, as stated, a liquefaction, and after it has

passed through the dividing wall, a solidification, occurs in each of the succeeding members of a string of cells. This is a very laborious and wearisome process, and the question involuntarily arises, after observing these methods of transmission, why these numerous partition walls in the rows of cells are not done away with. The wood vessels have been produced from rows of cells by the solution of the dividing partition walls; why are the many transverse walls retained here to complicate and retard the transportation of the substances? It must be supposed that these cross walls, which break up the free channel, are in some way beneficial to the plant, since they occur so generally and with such regularity. It might be thought, first of all, that these walls keep open the road, and that thereby the delicate walls of the cells forming the channel are protected from collapse. Apart from the fact that the cells of bast parenchyma, imbedded in niches and grooves in the periphery of the hard wood, are prevented from collapsing by their sheltered position and nevertheless exhibit transverse walls, while the delicate-walled laticiferous tubes, which are anything but well-protected, possess none and yet do not collapse—apart from this, such a delicate wall would form but a bad stiffening agent, and the support would be obtained much better by band-like circular thickenings. It has also been surmised that the cross walls inserted in the channels might be of use in that they prevent an excessive accumulation of solid bodies at certain places on the road. Where the cells of a cell-row stand vertically above one another, as, for example, in erect stems, it is found that the small starch-granules sink to the bottom of the cells and lie on the lower transverse wall. If all the solid corpuscles contained in the sap of a long vertical tube were to sink to the bottom, of course an obstruction might arise which would be anything but beneficial. But the significance of the partition walls most probably lies in the transformations they produce in the substances. It may be safely assumed that those materials which must pass through not merely the cellulose transverse wall, but also the protoplasmic parietal layer of the cell-chamber, undergo an alteration thus under the influence of the living protoplasm; that the position of the atoms becomes different, or that new atoms enter into combination and others are displaced, in short, that re-arrangements and transformations occur from which it results that the transmitted materials arrive at their destinations prepared in the best possible way. With this, however, we return to the important theorem previously stated, that these rows of cells have not merely the significance of a road along which the materials, formed at the starting-points, are conducted unchanged to the terminal stations; but that they also form places for the continuous transformation and alteration of these materials for subsequent use.

SIGNIFICANCE OF ANTHOCYANIN IN THE TRANSPORTATIONS AND TRANSFORMATIONS OF MATERIALS. AUTUMNAL COLOURING OF FOLIAGE.

In connection with the foregoing results of investigations into the transmission of substances, the fact must be noted that those agents which take part in the transformations of carbohydrates and albuminous substances are to be found all along the road which these follow and not merely at the beginning and end of the journey. Diastase, for example, is to be found everywhere along the strands of cells forming the path of the transitory starch, and when these strands run near the surface that colouring-matter called *anthocyanin*, a somewhat detailed description of which must be given, is also present.

In many instances the route of the travelling substances can be recognized by the naked eye, since it is coloured blue, violet, or red. Whether all these tints actually originate from one colouring-matter, which is red, violet, or blue according to the presence or absence of acids, has not been ascertained. The chemical composition of colouring-matters is yet little known, and it is possible that at present a whole group of them is collected together under the name anthocyanin. It is a matter of indifference with regard to the question in hand, as also is the question as to the way in which anthocyanin originates in plants. It need only be mentioned here that the statement according to which anthocyanin arises from the chlorophyll-corpuscles present in young plant organs cannot be correct in all cases; since this pigment occurs regularly in parasites entirely devoid of chlorophyll, in the Balanophoreæ, Rafflesiaceæ, and Hydnoreæ, in the Toothwort, in *Monotropa*, and numerous other plants destitute of green colour. In green-leaved plants anthocyanin is most usually met with in places which have little chlorophyll, or which have never possessed any, in flowers and fruits, along the ribs of leaves, and principally in leaf-stalks and herbaceous stems. In hundreds of species belonging to widely-differing families the leaf-veins and ribs, leaf-stalks and leaf-sheaths are coloured violet, red, or blue, and this colouring is co-extensive with the vascular bundles beneath them.

It is difficult to say whether anthocyanin exercises a photochemical effect on the travelling substances in the given paths, or whether it is only of use in that it keeps back the light rays which would decompose the travelling materials. In support of the latter view we have the fact that anthocyanin is much more abundantly deposited in paths exposed to the light than in those which are shaded, and that in shaded organs the same changes and transmissions of materials occur as in those exposed to bright light, where the superficial cells are coloured with anthocyanin, and where consequently the paths of the transmitted substances below are to some extent screened. It is noticeable that plant organs which are very thickly covered with hairs scarcely ever develop anthocyanin. From all this it may be concluded that anthocyanin, when it appears in places directly illumined by light rays, serves principally as a screen, *i.e.* as a protective agent or awning against injurious light rays.

Here another very remarkable phenomenon may be considered. If the colourless and scaly rhizome of *Dentaria bulbifera* be dug out of the dark forest soil, it appears beautifully white, as if carved out of ivory. If it is put in a glass vessel which is filled up with water and placed in the sun, so that the rhizome is illumined by the direct rays, the white scales in a very short time assume a slight violet tint, and in a few days the whole of the scaly rhizome becomes coloured a deep violet. The same thing happens with the rhizomes of several species of Cuckoo-flower, Violet, Toothwort, &c., but in these it is a little longer before the violet colour appears. The tissues brought from the darkness into the bright light try to neutralize the influence of the light which is injurious to certain substances, and therefore anthocyanin must not be regarded merely as an agent for protecting chlorophyll alone, but other chemical compounds also. That a far wider significance in the life of plants is also assigned to it will be demonstrated in the following section.

Very often anthocyanin only appears temporarily, when the transmission of food substances occurs on a very large scale. When seeds are germinated, and their reserve materials are conducted into the rapidly sprouting seedlings, such as those produced from the starchy seeds of polygonums, oraches, palms, grasses, &c., anthocyanin regularly appears, while later on it partly or wholly vanishes. When in spring the foliage-buds on subterranean root-stocks or branches begin to develop, and the materials stored in the stem structures travel into the young leaves, to be employed there in further construction, these leaves do not appear green in most cases, but reddish-violet or reddish-brown in colour. As instances of this may be mentioned the well-known Tree of Heaven (*Ailanthus glandulosa*), Walnut (*Juglans regia*), Pistacia (*Pistacia Terebinthus*), the Sumachs (*Rhus Cotinus* and *Rhus Typhinum*), the Judas Tree (*Cercis Siliquastrum*), Berberideæ (*Mahonia, Podophyllum, Epimedium*), Ampelideæ (*Vitis, Cissus, Ampelopsis*), the Trumpet Tree (*Catalpa syringæfolia*), the red-berried Elder (*Sambucus racemosa*), Cherry (*Prunus avium*), Peony and Sea Lavender (*Pæonia* and *Statice*), and Rhubarb and Dock (*Rheum* and *Rumex*). Later on, when the transmission is effected, when the foliage-leaves are developed and are able to act independently, the green chlorophyll appears; the leaves become green, and the anthocyanin either vanishes entirely or remains only in those places where it is required as a protection to the chlorophyll, or for another important purpose to be dealt with in the following section, viz. the transformation of light into heat.

In many plants, anthocyanin is again developed in great abundance when the leaves are obliged to stop their activity for a time on account of the commencing dryness of the soil, or still more, on account of cold and the consequent delay of supplies of crude sap. In order to describe this formation of anthocyanin and everything connected with it, it is necessary to go back a little, and to discuss, first of all, the metabolism and transport of materials connected with the stoppage of activity in the green leaves at the close of the vegetative period. These

differ essentially according as the leaves of the plant continue active through one, or through several vegetative periods, *i.e.* according as the leaves are deciduous or lasting but one year, or evergreen, that is to say, lasting for two or more years. Evergreen leaves are so organized in all those regions whose climate necessitates a temporary suspension of vital activity, that they may be able to survive the periods of drought or frost of one or even of several years without injury. Before they enter upon their summer sleep in regions of summer drought, or their winter trance in regions with cold winters, alterations occur in their cells, which, in the main, terminate in the diminution of the water contents and the formation of substances which will not be altered by the prevailing frost or dryness. In regions where we have a winter sleep, the chlorophyll-granules assume a yellowish-brown or brownish-red colour, and adhere together in clumps, which withdraw as far as possible from the surface of the leaf, travelling down to the floor of the palisade-cells and occupying their lower ends. These alterations are only slightly apparent outwardly in perennial leaves preparing for their winter period of rest; the only thing one notices is that the leaves, which in summer are a vivid green, exhibit a darker green, or incline to brown or yellow; which change of colour is observed to the greatest extent in *Thuja, Cryptomeria, Sequoia, Chamæcyparis, Libocedrus,* and generally in most evergreen conifers.

The changes which are accomplished in leaves lasting only one year, at the onset of the summer drought or winter cold, are much deeper rooted and obvious. These leaves are not clad so as to be able to defy the drought or frost, and are therefore thrown off at the commencement of the unfavourable period. If these leaves were to fall without further ceremony, all the substances in the tissues of the leaves, whose production entailed a considerable amount of work, would be entirely lost. But it is part of the economy of plants that such a waste is carefully guarded against. Before the leaves are detached, the carbohydrates and albuminous materials, in general everything which is of use to the plant, is conveyed from the leaf-blades into the woody branches or subterranean root-stocks, and there deposited in places where they find a safe resting-place, and can survive the drought of summer or cold of winter unharmed. In this way the plant suffers only the slightest loss in the materials manufactured by it in the preceding vegetative period; for the leaves from which everything useful has been transported into the stem-structures now form nothing more than a dead framework, and their cell-chambers contain only small yellow granules, together with crystals of calcium oxalate, which cannot be employed further, and are of no more use (see fig. 123 [1]). The shining yellow granules, which are found in the cells of fallen leaves, and to which is due the yellow colouring of autumn foliage, are to be regarded as the ultimate useless residue after the withdrawal of the transformed chlorophyll-corpuscles. The crystals of calcium oxalate have arisen in the formation of albumens by the decomposition of nitric and sulphuric acids. Both of them can be sacrificed. As a matter of

fact, the rejection of these structures is no sacrifice in reality, since they are only superfluous ballast by which, under certain conditions, the plants may be hampered in their next year's work, and of which they therefore rid themselves most seasonably and suitably. The fall of the leaf may be looked upon, so far, as an excretion of superfluous matter, which, in deciduous plants, occurs only once every year, but is then carried out on a grand scale. To the benefits which this wholesome excretion of waste, formed in the metabolism, affords to individual plants must be added the fact that the fallen leaf reaches the ground with its abundance of lime, decays there, contributes to the formation of humus, which contains calcium nitrate, and so becomes of use to the vegetable kingdom as a whole, as already described in detail.

The emigration of the useful materials from the leaf-blades to the store-rooms in the interior of the branches and root-stocks must, as a rule, be accomplished fairly quickly; most rapidly, of course, where the period of vegetation during which the foliage-leaves can be active is short, when the leaves are obliged to make use of the favourable time to the utmost, and where the change of seasons occurs abruptly. The materials withdrawn travel by the same route as in general is taken by the substances normally manufactured in the leaves. The accessories by which the carbohydrates and albumens to be removed are prepared for emigration, might (one would think) be the same in every case. But, just as in one species one kind, and in another a different kind are developed when the leaves are most active, so in different species at the close of the vegetative period, when the great emigration takes place, we have again various accessories, and various despatching and protective agents. In many instances the accessories are colourless, and are not recognizable by the naked eye even when developed in great quantity. It can only be seen that the leaves lose their fresh green on account of the change experienced by the chlorophyll bodies for the purpose of emigration, and that a yellowish tint appears instead of the green colour, which is produced by the already-mentioned yellow granules remaining behind after the departure of the chlorophyll-corpuscles. In many leaves the number of these yellow granules is so small that even the yellow tint is hardly apparent, and these leaves then are a dirty yellowish-white, shrivel up very quickly, and become brown.

Anthocyanin, however, is produced in many plants during the emigration of the carbohydrates and albuminous materials, and to such an extent, that it becomes plainly visible on the exterior. It appears red in the cell-sap in the presence of acids which occur very regularly as metabolic accessories in the autumn leaves, blue when no acids are present, and violet when the amount of free acids is but small. If there is an abundance of yellow granules together with the acid, red anthocyanin, the leaf assumes an orange colour. Thus the green colour of the foliage changes at the period of the great autumal emigration, sometimes into yellow, or brown, or red, violet or orange, and in this way we have a play of colour exhibiting the greater variety the more numerous are the plant species

growing associated together in the particular spot. If the leaves are thickly covered with silky or woolly hairs, or if the hairs are felted or peltate, anthocyanin is scarcely ever developed; but when the green tissue of these leaves becomes also changed in colour, the new tint can be seen as little as was the green previously, on account of the hairy coat over the coloured cells. Accordingly, such felted, silky, or scale-covered leaves remain grey or white even when they fall from the branches. If plants of this kind grow among others whose foliage is bare, their grey and white tints considerably increase the variety of the entire collection. But the greatest amount of colour is seen when the neighbourhood is sprinkled with plants having evergreen foliage; it may then happen that a relatively small space of meadow or wood appears decked in all the colours of the rainbow in the most manifold variety.

The splendour of colours exhibited by tropical forests, which is usually represented as much more magnificent than it really is, stands no comparison with that developed in autumn in the north temperate zone. The forests of firs and leafy trees on the mountain slopes along the Rhine and Danube in Europe, and on the shores of the Canadian lakes in North America at that season present a scene of entrancing beauty. The heights along the middle course of the Danube, for example, the region known as the Wachan, below the town of Melk, shows wide expanses of forests, in which beeches, hornbeams, evergreen oaks, common and Norway maples, birches, wild cherries and pears, mountain ashes and wild service-trees, aspens, limes, spruces, pines and firs take a share in the greatest variety. Bushes of Barberry (*Berberis vulgaris*), Dogwood (*Cornus sanguinea*), Cornel (*Cornus mas*), Spindle Tree (*Euonymus Europæus* and *verrucosus*), Dwarf Cherry (*Prunus Chamæcerasus*), Sloe (*Prunus spinosa*), Juniper (*Juniperus communis*), and many other low shrubs arise as undergrowth, and spring up on the margins of the forests. The mountain slopes abutting on the valleys are planted with vines, and near by grow peach and apricot trees in great abundance. In the meadows on the shore, and on the islands of the Danube, rise huge abeles and black poplars, elms, willows, alders, and also an abundant sprinkling of trees of the bird cherry (*Prunus Padus*). The nights are bitterly cold there; even in the middle of October, damp mists hover over the river, and hoar-frost covers the grassy regions at the bottom of the valley. But during the day it is still fairly warm, the morning mists are dispelled by the rays of the sun, a cloudless sky stretches over the landscape, and soft breezes, swaying the threads of the vagrant spiders, blow from the east through the river valley. The first frosts are the signal for the beginning of the vintage; all is busy in the vine-planted districts, and the call of the vine-dresser resounds from hill to hill. But it is also the signal for the forests on the mountain slopes and in the meadows to change their hues. What an abundance of colour is then unfolded! The crowns of the pines bluish-green, the slender summits of the firs dark green, the foliage of hornbeams, maples, and white-stemmed birches pale yellow, the oaks brownish-yellow, the broad tracts of forest stocked with

beeches in all gradations from yellowish to brownish-red, the mountain ashes, cherries and barberry bushes scarlet, the bird cherry and wild service trees purple, the cornel and spindle-tree violet, aspens orange, abeles and silver willows white and grey, and alders a dull brownish-green. And all these colours are distributed in the most varied and charming manner. Here are dark patches traversed by broad light bands and narrow-twisted stripes; there the forest is symmetrically patterned; there again the Chinese fire of an isolated cherry-tree or the summit of a single birch, with its lustrous gold springing up among the pines, illuminates the green background. To be sure this splendour of colour lasts but a short time. At the end of October the first frosts set in, and when the north wind rages over the mountain tops, all the red, violet, yellow, and brown foliage is shaken from the branches, tossed in a gay whirl to the ground, and drifted together along the banks and hedges. After a few days the mantle of foliage on the ground takes on a uniform brown tint, and in a few more days is buried under the winter coat of snow.

The autumnal colouring of the foliage in those parts of the North American forest regions, whose vegetation presents the greatest analogy to that of the Old World just described (*i.e.* in the neighbourhood of the St. Lawrence and from the Canadian lakes to the Alleghany Mountains), lasts much longer than in the forest regions of Central Europe. There also evergreen conifers grow side by side with deciduous trees, and there again a rich underwood flourishes in the forest regions. To some extent we have exactly the same species composing the woods—pines and firs, beeches and hornbeams, oaks, ashes, limes, birches, alders, poplars, maples, elms, hawthorn, guelder-rose, and dogwood; but the wealth of forms is far greater than in Central Europe. In the neighbourhood of the shores of Lake Erie, for instance (as represented in Plate V., entitled "Autumnal Tints on Lake Erie"), we have in addition to the trees enumerated the *Rhus Toxicodendron* and *R. Typhinum*, the Tulip-tree, Western Plane, several walnuts, robinias, *Gymnocladus*, *Liquidamber*, and especially some Ampelideæ which climb like lianes to the highest tree-top. This greater variety of species produces an even richer play of colour in autumn than in the central European districts. The change of colour of the deciduous trees begins in some species always at the commencement of September, and stretches over a whole month, so that the fall of the last leaves usually does not occur until about the middle of October. The American beech (*Fagus ferruginea*) changes colour exactly like the European; and the American birches (*Betula nigra* and *B. papyracea*) exhibit in their autumn foliage the same golden yellow as do their European allies; but the autumn foliage of oaks, which flourish with an extraordinary number of species south of the Canadian lakes, present every tint from yellow to orange and ruddy brown; the Red Maple (*Acer rubrum*) shrouds itself in dark red, the Tulip-tree exhibits the lightest yellow, the large-spined hawthorn bushes, the Sheep-berry (*Viburnum Lentago*) and the *Rhus Toxicodendron* become violet, the Sumach (*Rhus Typhinum*), and the wild vines (*Vitis* and *Ampelopsis*), climbing up the branches of the trees, clothe

them in flaming scarlet. With this gay assemblage of vivid colours the Canadian firs mingle their deep, dark green, and the Weymouth Pines the dull bluish-green of their needle-leaved summits. Where such a wood is developed with all its wealth of species, and where there is an opportunity of seeing it pass slowly under view in the soft light of a September day, as, for example, in a journey along the southern shore of the Canadian lakes, the eye revels in the changing pictures of scenery and in a wealth of colour such as it meets with in no other forest country.

Of course the autumnal colouring is not limited to the deciduous foliage of the trees and shrubs enumerated, but includes the perennial low shrubs and herbs. In forest regions, however, only the large forms of the greater trees stand out, and the low bush only rarely forms a characteristic feature in the autumn landscape. But where lofty trees are absent, and where the clumps of low plants are the characteristic feature, as in the regions of the Arctic flora, and especially in the mountain slopes above the tree limit, the matter is quite different. Of these latter regions, however, there is scarcely one which can rival the Alps of Central Europe in respect of the autumnal change of colour of the vegetation. It is especially in those parts of the Central Alps characterized by the great variety of their flora and their wealth of Ericaceæ, where strata of slate and limestone alternate or lie side by side, that the spectacle here described passes with a splendour of which the ordinary summer visitor to the Alps can form no conception. The time of commencement of the display cannot be definitely given; it varies from year to year according to the prevailing conditions of temperature and moisture. If even at the end of August fresh-fallen snow remains for several days on the slopes above the tree limit, the colouring may make its appearance as early as this; but if, as is usually the case, the heights do not assume their white mantle of snow until the middle of September, after a storm, and if during the latter half of the month the fresh snow melts and a clear sky prevails over the mountain heights, then the autumnal change of colour is retarded so much longer. Below, in the depths of the valley, which lie for wide expanses already in the shade on account of the low position of the sun, the ground remains continuously whitened by the frost, while up above, on the southern slopes of the mountain heights, the night's frost vanishes with the first glimpses of the sun, and soft breezes blow over them throughout the day. Ptarmigans and swarms of birds of passage journeying over the Alpine passes, but stopping here for a short rest, are busy in picking off the berries from the low bushes which cover the slopes in great abundance; but the butterflies which were so active in the summer among the Alpine flowers have vanished; here and there isolated scabiouses and the dark spikes of the late-blooming *Gnaphalium* still linger, but everything else is in fruit, and the procession of the flowers is past. And yet the slopes have all the brightness of summer meadows, which are adorned with innumerable flowers. The deciduous foliage of the low shrubs and herbs, and especially that of the stunted thick-carpeting bushes (whose materials are conveyed into the woody branches and underground stem-structures) attains even in this short time red, violet, and yellow tints, which are in no wise inferior

in glow and brilliancy to the most vivid colours of flowers. The deciduous whortleberries and a species of bearberry are most conspicuous. While the leaves of the Bilberry (*Vaccinium uliginosum*) assumes a violet colour, the red Whortleberries (*V. vitis idæa*) clothe themselves in deep red, and the Bearberry (*Arctostaphylos alpina*) in vivid scarlet. The autumnal leaves of these plants exhibit the most beautiful red observed in any autumnal foliage; it is much more fiery than in the North American vines and the sumach trees; and when the foliage of this Bearberry is illuminated by oblique sunbeams on a mountain slope, the observer below might fancy he saw flames of strontium forking up out of the ground. The leaves of many herbaceous plants also, such as Alpine geraniums and Alpine hawkweeds, become coloured with anthocyanin at the margins, and along the veins, or even over the whole surface, before withering; and seen from a distance, look like red, violet, and variegated flowers. The Alpine willows, however, especially the carpeting *Salix retusa*, and the low bush of *Salix hastata* and *S. arbuscula*, together with the red-fruited *Sorbus Chamæ-mespilus*, take a golden yellow. The latter chiefly border the water-courses, and on looking down from above on the gullies and ravines through which the water pursues its tortuous way, interrupted by small cascades, these bushes are recognized as a twisted, golden fretwork, thrown up against the darker background. Between the low undergrowth of whortleberries and bilberries, but principally between the low-lying sprays of Alpine bearberries, spring up everywhere white and grey lichens, especially the Reindeer-moss and the Iceland-moss, and some rocky ridges and slopes are so exclusively covered with these structures that they look from a distance like white patches and stripes on red, violet, and yellow grounds. The display of colours in Alpine regions is materially heightened by the fact that broad patches of dark tints are not wanting. The number of evergreen plants is comparatively large, and some of those species which appear in clumps retain their green foliage under the long-continued winter coat of snow until the vegetative period of the next year. The groups of mountain pines (*Pinus humilis, Mughus*, and *Pumilio*), the rhododendron bushes (*Rhododendron hirsutum* and *ferrugineum*), the tufts of Crowberry (*Empetrum nigrum*), and the glistening carpet of the evergreen Bearberry (*Arctostaphylos Uva-Ursi*), with their dark-green tints, bring a certain calm into the gay confusion. The carpets of *Azalea procumbens*, which in the autumn becomes brownish-green in colour, in consequence of the collection of the chlorophyll-corpuscles of the green leaf-cells into balls, also moderate the glare of the picture in a harmonious manner.

The charming spectacle of the colouring of deciduous foliage in Alpine regions as a rule only lasts for about a fortnight. If the slopes still remain free from snow for a short time, all the red, violet, and yellow leaves become detached from the twigs and branches. Whatever useful materials were still present in the foliage have emigrated during this time to the stem-structures, where they are to pass the winter; and the fallen leaves become brown and blackened. Soon the wintry pall of snow is spread upon the mountains; and the ridges, slopes, and hollows, from

which flamed so recently tints of red gold between the dark mountain pines, are now covered with dazzling white from the winter sky.

3.—PROPELLING FORCES IN THE CONVERSION AND DISTRIBUTION OF MATERIALS.

Respiration.—Development of Light and Heat.—Fermentation.

RESPIRATION.

One of the most remarkable things about metabolism in plants is that every species is its own model and type, that the compounds which are manufactured in various species always remain the same in successive generations, and that from the same soil, the same water, and the same air, under equal illumination and under the influence of the same temperature, the most different organic compounds are prepared by various species situated in close proximity. Within an area of a square metre spring up from the forest soil the poisonous *Boletus sanguineus*, the savoury Mushroom, and the latex-swollen *Russula*; and if the seeds of Mustard, Corn-cockle, and Poppy (*Sinapis nigra, Agrostemma Githago, Papaver Rhœas*) are strewn on a garden bed of uniform soil, so that the plants germinated from these seeds grow simultaneously side by side, their seeds will indeed exhibit materials of the most varied composition, but every mustard seed, every seed of the corn-cockle, and every poppy seed will present exactly the same compounds as were possessed by the seeds sown, compounds which the seeds of these species have contained for thousands of years. This phenomenon can only be explained by the association of like to like always and everywhere in the plant, and by the supposition that every molecule of a certain material not only operates as a centre of attraction on its surroundings, but that the attracted atoms are grouped according to the special type, just as happens in the crystallization of mineral substances.

If the atoms in the colourless cells of a seed germinating in the darkness of the soil are attracted in the manner indicated, arranged in a certain way, and connected together to form a solid body, the chemical equilibrium in those cells must be disturbed. If the materials thus attracted were previously dissolved in the sap of these cells, the degree of concentration of their sap must have been diminished in consequence of their withdrawal, and will be less than that of the neighbouring cells. But this dissimilarity cannot be maintained, and therefore a compensating movement occurs, which spreads to more and more distant cells; or, in other words, the materials stream towards the places of consumption. We return to this process, already once described, in order to review the propelling forces which are concerned in the metamorphoses and distribution of the materials.

The process of the combination of atoms into a solid body which we are now considering, for example, the formation of cellulose, is a performance of work combined with the fixation of sensible heat and with the transformation of kinetic into potential energy. But whence do the colourless cells derive their sensible heat and kinetic energy? When carbonic acid is decomposed and sugar or some other carbohydrate is formed in a green cell, a sunbeam becomes imprisoned and fixed. But this is not the case in cells devoid of chlorophyll, especially in those working in darkness under the ground. The protoplasm of these cells derives the sensible heat and kinetic energy which it consumes or renders latent from the sun, not directly, but by very indirect methods. It obtains them by a portion of the material conveyed to it becoming decomposed, by whose synthesis in the green cells above-ground the kinetic energy of the sun's ray has been changed into potential, and in this way the potential energy becomes again changed into kinetic, and the latent heat transformed into sensible heat. The materials which the green cells manufacture out of inorganic food would be merely an accumulated dead capital lying unused if they were to remain in the condition in which they had been formed. They must be turned to account, dissolved, transformed, and distributed; the impelling forces necessary for this are obtained by a portion of the material manufactured in the green cells undergoing a process which is exactly the opposite of that carried out in their formation. At the very time when carbonic acid is split up, oxygen given out, a carbohydrate formed, and heat rendered latent thereby, carbohydrates are being decomposed, oxygen taken up, carbonic acid excreted, and heat liberated. Of course this process of decomposition cannot extend to the whole mass of the materials manufactured by the green cells. It would indeed be absurd if in one part of the plant those materials became again disorganized and changed into air and water which in another part had been compounded of these same elements. As a matter of fact, this process of decomposition is limited to but a part of the materials produced in the green cells, and the whole process may be most correctly represented thus: one portion of the materials formed from inorganic food in the green cells is employed in the further growth of the plant body; but this further growth only becomes possible if the other portion supplies the forces necessary for the carrying on of the building. The one process is therefore just as important as the other; they mutually supplement each other, and this supplementing is one of the most important life-processes of plants.

It has been stated that in order to obtain the necessary impelling forces oxygen is taken in, the molecules it attacks are decomposed, and carbon dioxide is liberated. This process is therefore an oxidation, a burning of organic material, and is to be placed in the same category as the burning of carbohydrates, which occurs in animal bodies in respiration. It is called *respiration* in plants also, although here we do not find special localized respiratory organs as is usually the case in animals. In plants all the living parts can breathe, and to them the atmospheric air, that is to say, the oxygen contained in it, obtains access—

to roots and tubers, stems and foliage, fruits and seeds, green plants and parasites devoid of chlorophyll, plants with and without stomata, saprophytes and water plants. All these breathe as long as they are alive, and in plants no less than in animals breathing and living can be used as synonymous terms for all practical purposes. The first fundamental condition of respiration is naturally the presence of free atmospheric oxygen. When this is absent, plants, like animals, are suffocated and die. If plants are put under the receiver of an air-pump, from which the air is exhausted, or in a chamber filled with hydrogen, nitrogen, or coal-gas, the streaming movement of the protoplasm in the cells ceases in a short time, foliage and floral-leaves, if they exhibit phenomena of movement in the living plants, become rigid, and if kept for a longer period in the atmosphere without oxygen, the plants die. Even if again brought into air containing oxygen, they can no longer be resuscitated, but remain dead.

The parts of plants surrounded by atmospheric air are never in want of oxygen, but roots often get into an unfavourable position where the quantity of oxygen in the air of the soil is very small, or where the atmospheric air is replaced by other gases. This explains why plants do not prosper in so-called "dead" earth, and why the roots seek principally those loose places of the upper strata of soil which are porous and well-ventilated, and avoid the deeper-lying, badly-ventilated, dead ground. The decay of trees which have been planted in towns and parks near gas-pipes, whose roots have been surrounded with coal-gas for some time owing to a leak in the pipes, is also explicable in this way.

Aquatic plants take up the oxygen of the atmospheric air absorbed by the water. Where there is none, vegetable life under water becomes impossible. If anyone, when sending off water plants, tightly corks up the bottle after filling with the necessary water, under the impression that the plants, being still in their element, will thus bear the journey well, he will be sadly undeceived. The small quantity of oxygen in the atmospheric air contained by the water is soon exhausted, and the aquatic plants are suffocated within twenty-four hours, or even in a much shorter time, just like fishes which have been conveyed in a tightly-corked bottle of water.

All plants do not breathe with the same energy, and in any plant a great difference can be noticed in the respiration of the various organs. The floral-leaves, possessing no chlorophyll, respire much more vigorously than the green foliage-leaves; underground root-stocks, bulbs, and tubers, also without chlorophyll, to a much greater extent than the green stem. In the green organs of plants exposed to sunlight two processes are carried on, the formation and the splitting up of carbohydrates. The latter process, however, is so obscured by the former, that it can only be observed with difficulty. It has been estimated that in a laurel leaf the amount of carbohydrates formed in any given time is thirty times as great as of those decomposed, *i.e.* respired.

A great difference is also exhibited according to the stage of development of the individual plant organs. Roots, stems, and leaves breathe much more vigorously

when young than when fully formed. When seeds are allowed to germinate in damp earth, respiration is at first quite inconsiderable, but when the parts of the seedling begin to elongate, and when the stores of materials furnished by the parent plant are dissolved and used up, respiration becomes very energetic. Later on, when the seedling has grown up so far that it can itself work with the help of its leaves, which have meanwhile become green, respiration again diminishes. The same thing occurs in the development of buds; there, too, the young leaves just emerging from the covering of the bud breathe to a much greater extent than the fully-formed green foliage. That organs which have attained their full size, and are apparently quite inactive, still respire, is shown from the observation that roots and tubers which have been dug up in the autumn and left in a cellar through the winter exhale carbonic acid without any visible outward change. In beet-roots which have been dug up a 1-per-cent decrease of sugar, and an exhalation of carbonic acid corresponding to this decrease, have been observed within two months, a proof that change of materials and respiration can occur even in structures which lie dormant during the winter.

According to what has just been stated about the significance of respiration to the life of plants, it is quite obvious that the energy of respiration which is reckoned by the amount of carbonic acid exhaled from a certain organized mass, or better, by the amount of oxygen absorbed, becomes greater the more vigorously the plant grows, and the quicker it builds up its body, just as a machine requires more fuel the greater the results required from it. If fuel is wanting or not present in sufficient quantity the machine stops, or does not perform as much work as it should be capable of doing. It is exactly the same in living plants. If the respiratory materials are absent, respiration is discontinued even in the presence of oxygen, and life becomes extinguished. If the supply of these materials is insufficient the plants only prolong their existence with difficulty, and their growth will be insignificant in consequence of the insufficiency of materials for carrying on the work. When shoots sprout from the "eyes" of a potato, it is at the cost of the carbohydrates and other materials stored up in the tuber. If this sprouting occurs in the open and the shoots grow up into the daylight, their leaves become green and manufacture new carbohydrates under the influence of the sun's rays; and of these a portion is at once employed as fuel for the further construction of the potato plants, that is to say, it is respired. If, on the other hand, the development of shoots from potatoes takes place in a dark cellar, their leaves cannot become green, and consequently no carbohydrates can be manufactured. The shoots then only continue to grow so long as the respiratory materials stored up in the tuber last; when these are exhausted, respiration comes to an end, and the shoots die off.

An approximate idea of the significance of respiration as an impelling force in those changes of materials whose end is the further growth of the plant may be obtained from a consideration of the following figures. A cubic centimetre of carbon dioxide contains 0·5376 milligramme of carbon, whose burning furnishes

4677 units of heat. The mechanical equivalent of this is 1,987,725 gramme-millimetres. When a carbohydrate is respired, for every cubic centimetre of carbon dioxide exhaled a store of energy is obtained which is equal to 1,987,725 gramme-millimetres, and therefore by it a gramme weight can be raised to a height of 1987 metres. It has, however, been ascertained that seedlings of poppy (which, when subsequently dried, weighed 0·45 gramme) exhaled 55 cubic centimetres of carbon dioxide in 24 hours, and seedlings of mustard (which, when dried later, weighed 0·55 gramme) 32 cubic centimetres in the same length of time. It can therefore be easily imagined what a large store of energy is obtained by respiration, even although the result, in consequence of various interruptions and obstructions, should fall far behind this estimate.

In comparing the living plant to a machine heated by coal, and trying to measure the work performed by it numerically, we are justified by the analogy of the transactions in the two cases, which are obvious. The comparison suggests itself naturally from the fact that in both cases similar impelling forces come into play, and that in both the necessary store of vital force is obtained by the combustion of carbon. Yet, on the other hand, combustion in a machine and respiration in a living plant are widely different. The peculiarity of plant respiration lies in the fact that materials are combined with the oxygen of the atmospheric air which would not enter into combustion with it at ordinary temperatures outside the living plant. Neither carbohydrates, fats, nor albumins, which are either directly or indirectly affected in respiration by the process of combustion, undergo, outside the plant cell, the alterations and decompositions which are carried on within it, and it may be taken as an established fact that oxygen only operates on them when conveyed to them by means of the living protoplasm. The effect of the transmitted oxygen is also restricted by the living protoplasm to the carbohydrates and other non-nitrogenous compounds which it incloses. Nitrogenous compounds are not respired directly, and the quantity of nitrogen in breathing plants is not lessened. We can only imagine these remarkable correlations as occurring in the following manner. The starch grains and droplets of oil are first rendered soluble, and are then oxygenated by the oxygen brought by the protoplasm; the albumins, on the other hand, are first split up into asparagin and a carbohydrate. The latter alone becomes oxidized, for the nitrogenous asparagin is not only not burnt, but is reconstructed into albumin, with the co-operation of the sun's rays, by attracting the newly-formed carbohydrates of the green cells and combining with them.

If we adhere to this view, it at once becomes evident how important is the co-operation of respiration and the formation of fresh carbohydrates in the green cells. If, in a plant, the production of new carbohydrates should be suspended, the reconstruction of albumins cannot ensue. At first all the respirable materials which yet remain in the plant are used up for the continuance of action, but if the formation of fresh carbohydrates remains unaccomplished, and even the last reserves are consumed, then the plant becomes exhausted, and ceases to breathe

and live. It has been estimated that a plant, in which the supplies of freshly-formed carbohydrates are lacking, can consume over 50 per cent of its substance by respiration before it perishes from exhaustion. This is the case, for example, in the potato-tubers mentioned, whose stems, developed in dark chambers, become overgrown, *i.e.* elongate exceedingly, while their rudimentary foliage-leaves remain very small and destitute of chlorophyll. Here, in the dark, no new formation of carbohydrates occurs, but respiration continues as long as any respirable materials yet remain. At length, when everything that can be made use of in this way is consumed, the shoots die off. Their dry weight, however, is only half as much as was that of the tuber from which they sprung; the other half has been completely burnt, *i.e.* changed into carbonic acid and water, which have rapidly evaporated.

Sunlight is not necessary to respiration, although without it the decomposition of carbonic acid and the formation of carbohydrates cannot take place. Breathing can be carried on in complete darkness. Underground organs: roots, tubers, bulbs, rhizomes, runners, likewise the mycelia and fruit-stalks of the plants classed together as fungi, as well as seeds buried in the earth—all these normally breathe in darkness. Respiration continues throughout the darkest night. That growth, the most important of all the processes stimulated by respiration, is restricted by the influence of light, will be discussed when describing growth; concentrated light produces a rapid oxidation and disorganization of the organ exposed, which, however, must not be looked upon as the respiration of the plant.

DEVELOPMENT OF LIGHT AND HEAT.

It is to be expected that respiration will be more vigorous in plants the higher the temperature, since the process of respiration is a combustion of carbon compounds, and all combustion is helped by a rise of temperature. As a matter of fact, it has been observed that the exhalation of carbonic acid (that is to say, respiration) also increases with rise of temperature. Of course this is true only up to a certain point. Respiration may commence even at 0°, and reaches a maximum between 15° and 35° C. according to the species, but beyond that it quickly diminishes. It entirely ceases at temperatures which produce coagulation of the proteids, and which are followed by the death of the living protoplasm.

When once respiration is started, the oxygen necessary for the combustion of carbohydrates is derived from the surrounding atmospheric air. But the first incitement to respiration does not proceed from this, or in other words, the absorbed oxygen does not furnish the first stimulus to respiration. Dead plants into which oxygen is made to enter do not breathe any more than do butterflies which have been suffocated by withdrawal of oxygen, and then subsequently brought into the fresh air. Oxygen cannot produce those movements of the atoms which are peculiar to life either in plants or animals which have been completely suffocated. Since only living plants can breathe, respiration must be brought about by a force which is liberated in the living protoplasm, by that

specific force which must be designated as vital. The first movement, *i.e.* the first chemical process with which respiration commences, seems to be a splitting up of the albuminous molecules in the living protoplasm, the same process as that by which albumen is separated into asparagin and a carbohydrate, perhaps into asparagin, a carbohydrate, and carbon dioxide. The next thing, of course, would be a withdrawal of oxygen from the air, but it should be noted that this is only for the purpose of continuing the metabolic changes, which have originated spontaneously in the living protoplasm.

Heat likewise is liberated in all combination of oxygen with other substances, especially in every combustion of carbon compounds. This heat is not always easily demonstrable in the plant organ in which it is set free. The heating of the respiring tissue is counteracted by the evaporation of water and by radiation in organs above-ground, particularly in the flattened, outspread foliage-leaves. Carbon is also reduced in the green foliage during the day under the influence of sunlight, and this is a process which goes hand in hand with the fixing of sensible heat. Now, since this process masks the respiration in the green leaves to a certain extent, it is intelligible that the heat liberated by respiration in these organs is but seldom perceptible, and that as a rule green leaves actually feel cool. It is even probable that the pleasant coolness under a shady canopy of leaves is not solely due to the interception of the sun's rays, but that the imprisonment of these rays and the fixation of heat during the manufacture of the primary carbohydrates also shares in the cooling of the air surrounding the leaves. But where these conditions are out of the question, the heat liberated can be demonstrated in respiring vegetable organs just as in animal bodies; and if respiring green leaves could neither transpire, nor radiate heat, and if, moreover, a supply of carbohydrates were stored up in them, the heat liberated by respiration would make itself evident in the immediate neighbourhood. This applies still more to subterranean bulbs and tubers in which transpiration and radiation are not only partly or entirely absent, but which are incapable of manufacturing carbohydrates for themselves as they have no chlorophyll, and which, consequently, render no heat latent.

Germinating seeds, and seedlings without chlorophyll behave in the same way as these respiring underground organs, provided that they are protected against evaporation and radiation. Barley-corns which have begun to germinate and are respiring vigorously raise the temperature of their environment quite noticeably if they lie heaped together so that the heat liberated becomes thus concentrated. It is well known that malt is germinated barley, and in the preparation of malt heaped-up barley-corns are caused to germinate. In this process the temperature of the immediate neighbourhood rises 5–10° C. above the temperature of the air which surrounds the piles of barley-corns outside. The liberation of heat in fungi is also very instructive. These derive the organic compounds from which they build up their mycelia and fruit bodies from other living organisms, or from the decaying remains of dead plants and animals. The receptacles often

develop very rapidly to a considerable size, and connected with this rapid growth there is always a rapid movement of the food absorbed by the mycelium, combined with an energetic respiration. Respiration is carried on chiefly at the periphery of the receptacle—in the mushrooms especially in the hymenial layer, which is very well protected from evaporation and radiation by its position on the lower side of the cap. Transmission of the food, and in particular of a large amount of water, takes place through the stalk which bears the cap. Numerous observations of fungi growing in their natural free condition, and rising but little above the soil, have invariably shown this result: the rise of temperature in the tissue of the cap is most pronounced where respiration is carried on most actively, *i.e.* in the hymenial layer. It is less in the central portion of the cap, and least in the stalk, through which the watery fluid travels at a temperature which differs but slightly from that of the surrounding earth. Respiration, of course, cannot be considerable here. For example, in *Boletus edulis,* from its size and shape particularly well suited for these investigations, the following results were obtained while the temperature of the surrounding earth was about 13° C.: temperature of the stalk, 14·2–15·6°; temperature of the body of the cap, 15·2–16·8°; of the hymenial layer, 16·7–18·1°. Further developed (but still quite fresh) fructifications exhibit higher temperatures than younger ones which have just appeared above the ground. Observations on other fungi of the Hymenomycetes yield like results. When the temperature of the surrounding earth was 12·2° *Lactarius scrobiculatus* exhibited in its stalk a temperature of 14·8°, and in its cap of 16·0°; *Amanita muscaria* in its stalk 14·2°, and in its cap 15·2°, while the temperature of the surrounding soil was 13·0°; *Hydnum imbricatum,* 13·0° in the stalk and 14·5° in the cap, while the surrounding earth showed a temperature of 12·2°. The peculiar shape of the cap in these last-named fungi is not well adapted to a separate measurement of the temperature in the body of the cap and in the hymenial layer, but it is probable that a slight difference exists between them, similar to that found in *Boletus.* The puff-balls belonging to the Gasteromycetes also exhibit a considerable rise of temperature above that of their surroundings in the respiring portions of their fructifications. Thus in *Lycoperdon cœlatum* a temperature of 15·8° was observed in the spherical receptacle shortly before dehiscence, while the temperature of the surrounding soil was only 12·2°.

The liberation of heat appears especially noticeable, too, in respiring flower-buds and in the rapidly-growing stalks which bear them, as well as in opened flowers. If the flowers are small, and if there are but few of them at the end of the stem, or if only a single small flower is borne at the end of a delicate stalk, the heat liberated may easily escape observation; but under very favourable conditions it makes itself readily manifest, and gives rise to a phenomenon so strange and unintelligible that everyone on observing it for the first time is surprised and puzzled. I refer to the fact that small and delicate flowers grow buried beneath the snow, and obtain the space they require by melting the hardened snow. The Alpine Soldanella is a very marked instance in point. As the snow melts and the

tricklings therefrom moisten the earth below, the Soldanella plants are aroused from their winter's rest. Their little arched flower-stalks begin to elongate and come into contact with the hard under surface of the snow, though the temperature here is zero. Growth is carried on at the expense of the supplies of materials obtained by the Soldanellas in the previous summer, which had been stored up partly in the evergreen leathery leaves lying flat on the ground, and partly in the short root-stock embedded in the soil. The reserves are employed as substances for building, and a portion of them is respired, in order that it may be possible to dissolve the rest, to bring them to the places where they are required, and to obtain the force necessary for the work. The heat liberated by this respiration melts the granular ice covering in the immediate neighbourhood of the flower-buds. In consequence of this a cavity is formed in the ice above each bud, or rather, each bud becomes overarched as if by a tiny dome of ice. But the stem continues to grow in height; and the flower-bud borne on it, which is respiring and giving out heat, is accordingly raised up in the dome-shaped hollow space and pushed into it. There it promotes afresh the melting of the ice and an extension of the cavity, and thus actually bores a path for itself upwards through the ice-strata. This goes on until at length the respiring and heat-producing Soldanella bud has melted an actual canal through the covering of hardened snow, and makes its appearance above, the stem looking as if it had been stuck into the snow. The flower-buds now open and the pretty violet bells sway about in the wind. Naturally the snow will be penetrated first where it is thinnest, *i.e.* near the margin, where also the melting from above proceeds most rapidly. Consequently it is the edge of the snow-field mainly which is riddled, the Soldanellas growing up through the holes. It is not at all uncommon to find places where 10–20 flowers appear on the border within a stretch a metre long. On looking closer and making cuttings through the ice, all the stages of development described may be seen side by side. Two other phenomena, however, are not a little surprising. Here and there are to be found single Soldanellas whose buds have already opened before they have emerged above the ice-covering. These Soldanellas actually blossom in a small cavity of the ice, and remind one of plant-organs or insects inclosed in amber or small coloured splinters which have been fused inside glass balls. This sub-glacial blossoming of the Soldanellas is not limited, strangely enough, to the opening of the corolla; the anthers actually dehisce and liberate their pollen.

What also surprises us very much on closer inspection is the fact that the holes in which the flower-stalks are situated narrow like a funnel towards the base, so that there the ice touches the stem, or, in other words, that the canal down below is completely filled by the stem. When it is remembered that the flower-bud which melted the ice and formed the canal had a diameter at least three times as large as that of the stem, it would be expected that the stem would be placed in the centre of a comparatively wide hole. But, as stated, this is not the case, and the phenomenon can only be explained by supposing that the porous granular ice forms a plastic mass, and that the granules displaced by the melting sink down in accordance

with the law of gravitation, unite together where a boring has taken place, and again form a compact mass in consequence of the regelation of the lower strata. It has still to be mentioned that the green leaves of the Soldanellas, which lie flat below the snow and ice, becoming flaccid during the growth of the flowers, and that the reserve materials stored up in them are completely used up by the growing stem and flowers. The green leaves then become wrinkled and perish, while new leaves develop after the snow has melted. These provide themselves with reserve food in order that in the next period of vegetation the growing stem and flowers may be efficiently nourished.

Here and there with the flowers of Soldanellas are found the young, but nevertheless yellowish-red, foliage-leaves of *Polygonum viviparum*, which grow up from below into the ice, and occasionally melt holes in it close to the edge of the snow-field. The white flowers of *Ranunculus alpestris* growing in company with the soldanellas in the same habitat have, on the other hand, not attained to the capacity of growing through the ice, and need as an incitement to growth a temperature which is rather above 0° C.; in consequence of which they always open their flowers first in places from which the snow has vanished a short time before.

The amount of the heat set free by the small flower-buds of soldanellas might be estimated by the quantity of ice melted, but so many sources of error enter into a calculation of this kind that the numbers obtained cannot lay claim to much accuracy, and we must be satisfied with the fact, even although it is not verified by figures based on a calorimetric experiment.

The melting of the ice by the heat liberated in the respiration of soldanellas is also of the greatest interest, since it furnishes a proof that single, small, extremely delicate flowers warm not only their own tissues but also their environment, and that the heat liberated in them does not become perceptible only because, as already remarked, it is counteracted by evaporation and radiation which are carried on at the same time, and because the respiring flowers are usually surrounded by atmospheric air, *i.e.* by a medium which is movable, fluctuating, and unstable. The air which in one moment is warmed by the respiring leaves is carried far away in the next instant, and is replaced by other air. This is the case especially in shallow flowers with recurved leaves, or in salver-shaped corollas widely opened above, round which there cannot be said to be any stagnation of air. But if the flower has the form of an inverted bell, as in the Foxglove, Gloxinias, and most campanulate flowers; if the floral-leaves bend upwards like a helmet, as in the Monkshood; if the flowers are tubular, inflated at the base like a flask, or pitcher-like as in Aristolochias, or form deep goblets as in the Cactaceæ and many gourds—then the air in the inclosed space is scarcely at all disturbed, there is stillness within the flower, the air there collected and warmed is retained almost unaltered in its quiet corner, and is not very easily replaced by other air.

On cool days a rise of temperature above that of the surrounding air can be usually perceived in the interior of such flowers, even when they stand quite alone. In an Alpine meadow the interior of a flower of *Gentiana acaulis* in the morning

shortly before sunrise exhibited a temperature of 10·6° C. when the temperature of the surrounding air was 8·4°. On a mountain meadow under a cloudy sky and in calm air the interior of a flower of *Campanula barbata* showed a temperature of 16·6°, and not far off on the borders of a forest the interior of the helmet-shaped sepal of *Aconitum paniculatum*, 14·6°, while the temperature of the outside air in both instances did not exceed 13·2°. The temperature of the air in the neighbourhood of a respiring plant shows a much greater rise if numerous, small, thickly-crowded flowers are inclosed in a common sheath, and especially when the space inclosed is undisturbed. In the same mountain meadow in which the temperature of the interior of the ball in the above-mentioned campanula (*Campanula barbata*) was tested, the Carline Thistle (*Carlina acaulis*) was also in full bloom. As the sky was cloudy, the capitula were closed, *i.e.* the apices of the stiff, involucral leaves were bent together, and formed a hollow inverted cone over the flowers. A thermometer placed between these bracts and pushed down as far as the flowers, showed a temperature of 20·4°, the temperature of the surrounding air being 13·2°, the difference, therefore, was more than 7° C.

In palms, whose numerous small crowded flowers are covered by large floral sheaths or spathes, the air within these coverings exhibits a rise of temperature which is so noticeable that it can be felt by placing the bare hand inside. The same thing occurs in the aroids. Here numerous small flowers are united into a spike on a thick fleshy axis, forming the so-called spadix, and each spadix is surrounded by a bract which at first is twisted together like a conical paper bag, being often distended like a barrel or inflated like a bladder. It is soon formed into the characteristic shape, but always incloses a cavity whose air is hardly ever disturbed by the influence of other air currents. With care a thermometer may be introduced into this cavity, and the temperature shown by it may be compared with that of the surroundings. For example, it was found when the temperature of the outer air was 25°, that in the interior of the spathe of the Brazilian *Tornelia fragrans* was almost 38°. At the same air-temperature the interior of the spathe of *Arum cordifolium*, in the island of Bourbon, exhibited a temperature of 35–39°. But the highest temperature has been noticed in the Italian Arum (*Arum Italicum*). This plant is very common in the region of the Mediterranean flora, and is frequently to be met with in vineyards under bushes, and even in hedges and roadsides. Its spadices, surrounded by large pale-green spathes, push their way in the spring through the soil like inverted conical bags; the spathe begins to open between 4 and 6 o'clock in the afternoon, and at the same time a peculiar fragrance, like wine, becomes noticeable in the neighbourhood of the plant. If a thermometer is introduced into the cavity of this spathe, it is shown that while the temperature of the outside air is about 15°, that in the interior has risen to 40°, sometimes even to 44°. These Aroideæ therefore exhibit a temperature in the neighbourhood of their respiring flowers which exceeds that of blood-heat.

In proportion as the energy of respiration increases with the rising temperature of the surrounding air from morning till afternoon, the temperature in the interior

of the flowers also rises, as shown by the following observations which were conducted in a place in the garden shaded from the direct influence of the sun's rays:

Temperature in the interior of the bell-shaped corolla of the Red Foxglove,	8·8°	15·2°	17·7°	20·0°	21·2°
Corresponding temperature of the surrounding air,	8·7°	15·0°	17·2°	19·1°	19·5°
Difference,	0·1°	0·2°	0·5°	0·9°	1·7°

While the liberation of heat occurs in all living plants, and is a natural consequence of respiration, *i.e.* of the combustion of carbon compounds, the development of light, which in other respects appears to be in many ways connected with the processes of combustion, is observed in living plants but seldom. It is only recognized with certainty in the Hymenomycetes, a group of fungi in which the rise of temperature during respiration has already been described. But even of these Hymenomycetes only relatively few are luminous, and these few only in certain stages of development. Most frequently the luminosity occurs in the mycelium of mushroom-like forms (*Agaricineæ*), which permeate the wood of old tree-trunks and the creeping roots of trees on the surface of the damp forest ground. This mycelium forms thicker dark strands, frequently joined together by cross-connections, which penetrate principally between the wood and the cortex, and these form most characteristic nets and lattice-works; it also consists of very slender dark threads, which take up their position in the wood usually at right angles to the long axis of the trunk; and, finally, there are extremely delicate colourless threads which grow through the woody cells in the manner shown in fig. 32. These actually permeate the entire wood, and are only perceptible to the naked eye when they are woven into net-works, and then are seen as whitish fringes and membranes situated on the sides of the holes formed in the disorganized wood.

It is these fine threads and webs of the mycelium which exhibit the remarkable illumination. Where they completely invest the wood-cells, it looks as if the wood itself were luminous, and we commonly speak of luminous wood and the luminous decay of tree-trunks. There is no doubt that the luminosity is exhibited by the mycelia of various agarics, which destroy the wood of firs and other foliage-trees. Usually the Rhizomorph (*Agaricus melleus*) is alone pointed out as the cause of the luminosity in wood, since this species is widely distributed; and where it has established itself sends up every year many receptacles, so that there is no difficulty in determining the species. But since luminous wood is also observed in the pine forests of higher mountain districts where the Rhizomorph is no longer found, it must be concluded that the mycelia of various other agarics, whose species cannot be determined on account of the absence of fructifications, exhibit the same phenomenon. The light is best seen in the open, in midsummer and autumn, after many days of wet weather, when the wood permeated by the mycelium has been moistened by the rain. But the moisture absorbed by the wood must not exceed a certain amount. Too much saturation prevents the phenomenon of luminosity just as much as excessive dryness. If the wood is removed from the place where it shines so well, the luminosity rapidly diminishes,

and ultimately entirely vanishes, although apparently the relations and conditions of life are exactly the same as before. I have repeatedly taken up luminous wood at night, and having brought it home, have tried to reproduce as far as possible the conditions under which the luminosity existed in the open; in the first night the light was unweakened, but after twenty-four hours it had usually disappeared entirely. If the luminous wood is placed in a closed space where the renewal of the air, *i.e.* of oxygen, is not carried on to a sufficient extent, the luminosity soon ceases. A rise of temperature is not favourable to its continuance, principally from the fact that a higher temperature brings about an alteration in the hygrometric condition of the wood. In pure oxygen the wood shows a decrease rather than an increase of light. In the depths of the forest the luminosity may be observed day after day for more than a week on the same trunk, if the conditions of humidity remain the same.

It is difficult to compare the light emitted from the mycelium with any other. It is not so green as that of glowworms, and has not the brilliancy of the phosphorescence of the sea; it is a dull white light. It most resembles that of pure phosphorus held under water. In the gloom of the forest it has a strange and therefore uncanny appearance, and the "will-o'-the-wisp" may, in part at any rate, be attributed to luminous wood. If a decayed tree-trunk penetrated by the light-giving mycelium is vigorously struck, so as to split it into hundreds of fragments, which fly out in all directions and fall scattered on the ground, each splinter becomes luminous, and the dark forest ground seems to be strewn with dots of light. The luminosity of these fragments, however, comes to an end before the next night.

The Rhizomorph and other allied agarics only exhibit the luminosity in their mycelium, their fructifications remaining dark under all circumstances. In a series of other agarics, viz. in the Brazilian *Agaricus Gardneri*, in *Agaricus igneus*, a native of Amboina, in *Agaricus noctilucens*, living in Manila, and in *Agaricus olearius*, which is widely distributed through the Mediterranean floral district, the actual fructifications emit light, usually from the hymenium developed on the under side of the cap, but more rarely the stipe also which bears the cap. The light produced by these fungi is like that from the mycelium of the agarics described previously, and the external conditions under which it occurs are also similar, except that the hygrometric state has not such a noticeable effect on it as on the luminous wood permeated by mycelial threads. At least in *Agaricus olearius*, a mushroom which grows among the roots of olive trees and forms its golden-yellow fructification in late autumn, the luminosity is to be seen equally well in dry and wet weather. As soon as the temperature falls below $+3°$, the light immediately ceases; it is best at 8–10°, and under higher temperatures it does not increase but gradually diminishes. If oxygen be kept away or withdrawn from the air, the luminosity immediately vanishes, but as soon as the atmospheric air is again restored, the phenomenon reappears. Dying agarics become less and less luminous, and their light is extinguished at their death. It is to be noted that not only agarics with luminous hymenia, but also those with luminous mycelia, emit light both by day and night.

On fine days in the open the light is not seen, but as soon as these structures are brought into a dark room, the phenomenon of light is to be seen, even during the day. The luminosity of the night is not increased by sun-illumination during the day, and consequently the phenomenon has nothing in common with that peculiar phosphorescence exhibited during the night by fluor-spar, which has previously been exposed to sunlight.

There are certain organic substances which shine in alkaline solutions when oxygen is present. It seems natural to suppose that such materials are formed in the agarics mentioned, and that oxygen is conveyed to them in respiration, thus producing the phenomenon of light. At any rate this would be the simplest way of explaining the luminosity. As to the advantage accruing to the plant itself, we can only form surmises. It seems most probable that the fungus-flies and beetles which deposit their eggs in the mycelia and fructifications of Hymenomycetes, and which are connected with the distribution of their spores in a manner to be described in detail later, are thereby guided to the fungi in the dark of night. Many of these flies and beetles only fly at night, and, like so many winged nocturnal animals, direct their path towards a luminous object. It may be, therefore, that the light proceeding from the agarics cited serves as an allurement and guide to the night-flying insects, just as the odour and brilliant colouring of other Hymenomycetes attracts the fungus-flies and beetles which swarm in broad daylight.

FERMENTATION.

About thirty years ago the difference between plants and animals was formulated as follows:—Plants transform kinetic into potential energy, and form organic compounds by the reduction of inorganic food, especially from carbonic acid, nitric acid, and water; animals transform potential into kinetic energy, and decompose and burn by respiration the organic compounds, formed by green plants, which serve them as food. This distinction, however, only holds good in part. On the one hand, plants devoid of chlorophyll are not taken into consideration, and on the other, it has been established that green plants also breathe, and therefore transform potential into kinetic energy. The respiration of plants does not differ either in its method or in its object and significance from that of animals. In both cases the living protoplasm withdraws oxygen from the air in order to convey it to certain expressly prepared carbon compounds which have been rendered combustible, and in both cases these carbon compounds are burnt in order that the necessary impelling forces may be obtained for further life and growth. But the analogy between plants and animals holds still further in this respect. When animals which are tenacious of life, *e.g.* frogs, are placed in an atmosphere containing no oxygen, they do not immediately perish, and do not at once cease to exhale carbon dioxide, consequently they still convert a certain amount of potential energy for a short time, by the combustion of carbon compounds in their bodies. They cannot derive the oxygen necessary for this from the surrounding air; there

is nothing left for them except to obtain it from the organic compounds of their own bodies. This cannot be carried on permanently, and if the frog is kept for a long time in an atmosphere without oxygen, it will at length die. For a short period, however, it is able to prolong its life in the way indicated. Exactly the same thing is seen in plants. When placed in a chamber from which free oxygen is absent, they do not immediately die, but endeavour for a short time to retain their life by utilizing combined oxygen, by withdrawing it from nitrates which have been absorbed with food, or from the organic compounds of their own bodies, richly furnished with oxygen. The oxygen obtained in this way is able to replace that usually derived from the environment, and can also bring about a combustion of carbon compounds; it can therefore provide the kinetic energy necessary for the continuance of life. Carbon dioxide is then exhaled from plants, even in an atmosphere without oxygen, and heat is liberated just as in normal respiration. But this abnormal source of energy does not last very long. If free atmospheric oxygen continues lacking, the plants exposed to such unaccustomed conditions at length perish from exhaustion and suffocation.

But it is also possible that living plants may exist in a region which is indeed devoid of free oxygen, but in which combined oxygen is present. Let us suppose that a plant, hitherto surrounded by atmospheric air from which it obtained free oxygen for use in respiration, has been plunged into a sugar solution, in which, of course, free oxygen is absent, but which contains a large quantity in combination with carbon and hydrogen in the form of sugar. Would such a plant be able to wrest the oxygen from the sugar and to utilize it for itself? In most cases certainly not. But in a few instances the living protoplasm has the power of splitting up the fluid oxygen-containing compounds with which it comes into contact, and can so obtain the oxygen necessary for the continuance of its life. It can also make use of other materials liberated from combination in the decomposition. This process has the greatest resemblance to respiration, carbon compounds are actually burnt with the help of the derived oxygen; carbon dioxide is exhaled, and heat is liberated. The plant, the living protoplasm of which accomplishes all this, maintains itself alive, prospers, and even grows and multiplies in a surprising manner. This process, however, is not called respiration, but is known as *fermentation*.

Of course the plants producing fermentation must not be supposed to include large leafy structures. On the contrary, they are all very insignificant and belong exclusively to spore-plants which are devoid of chlorophyll, and which are generally classed together under the name of fungi. In particular there are the four allied families, Bacteria, Yeasts, Moulds, and Basidiomycetes, of which many species in certain stages of development are capable of inducing fermentation.

Bacteria, which are also called Fission-Fungi or Schizomycetes, are the smallest of all living organisms, and the question has repeatedly arisen as to whether they are to be regarded as independent organisms, or as organized portions of dead, decomposing protoplasm. The discussion of this question will be left to the second

volume. Here it is sufficient to remark that bacteria appear as spherical, oval, or rod-like cells, which develop by repeated transverse division into chain-like or filamentous structures, very much resembling hyphal threads. These chains of cells break up, however, sooner or later, into their individual members, and then look as if they had been split into fragments, this appearance accounting for their name of "Fission-Fungi". In this way arise colonies of irregularly accumulated cells which are frequently embedded in a mucilaginous matrix. Many bacteria can live and multiply without taking free oxygen from the air. They obtain the materials necessary for this by setting up a fermentation in their immediate neighbourhood, *i.e.* a splitting up of carbohydrates and nitrogenous compounds. Fermentation gives rise to very different products, and makes itself evident in very different ways, according to the composition of the body attacked by the bacteria, and according to the species to which the bacteria, which are commencing their destructive activity, belong. In many instances pigments are produced, in consequence of the decomposition, which colour the attacked body yellow, red, violet, or blue; at another time, as, for example, in the souring of milk, a molecule of milk-sugar is decomposed into two molecules of lactic acid; or, by the ferment action of the *Bacterium aceti*, acetic acid is produced from alcohol; again in another instance, sugar is split up into dextrin, mannite, and carbonic acid, by a species of Bacterium, in the so-called viscous fermentations. One of the commonest fermentations is that to which albuminous compounds succumb, known as *putrefaction*. The albumens are decomposed by the action of one or perhaps several different species of bacteria into tyrosin, leucin, various amines, volatile fatty acids, ammonia, carbon dioxide, sulphuretted hydrogen, hydrogen, and water; and some of these make themselves evident by their offensive odour in a most unpleasant manner. To this class, too, belong the most notorious of all bacteria, which give rise to a decomposition of the liquids in living human and animal bodies, which deprive the blood of oxygen and bring about in it various other decompositions of organic compounds, and which are regarded as the cause of epidemic and endemic diseases. Contagions and miasmas are indeed for the greater part, if not wholly, bacterial, and the species which produce splenic fever in ruminants, diphtheria, small-pox, and cholera in man, are of such great interest that a whole section will be dedicated to them in the next volume.

The various species of yeast, which are called *Saccharomyces*, consist of spherical or ellipsoidal cells, which are much larger than the cells of bacteria, and also multiply in quite another way. They increase by sprouting, *i.e.* knob-like outgrowths arise on the surface of the multiplying-cells which rapidly enlarge, so that each outgrowth in a very short time is equal in size to the cell from which it originated. The daughter-cell thus formed is detached from the parent-cell, and may now itself produce daughter-cells by sprouting. Occasionally several successive buddings remain joined together, and then form colonies which somewhat resemble the prickly pears or opuntias in miniature. Yeast produces alcoholic fermentation. It causes grape-sugar to split up into alcohol and carbon

dioxide, the process also giving rise to a small quantity of succinic acid and glycerine. This fermentation is never very noticeable in living plants in free nature; there it is at any rate only carried on to a small extent. It is very important in the extensive artificial production of alcoholic beverages, for example, of wine, cider, beer, brandy, "pulque", rum, and many more, from grapes and other fruit, and from grape-sugar, obtained from starchy seeds, tubers, and roots.

Moulds consist of colourless, elongated, thin-walled cells, which appear to the naked eye like extremely delicate threads. These divide up by the intercalation of transverse walls, but they do not separate into their individual elements like the bacteria. The threads multiply very rapidly, and frequently numerous threads are crossed and intertwined like the threads of a cobweb, forming a loose, white net-work. They generally dwell on damp or fluid substrata, and closely invest them with their crowded threads. They also penetrate into the interior of these substrata. The cells which make their way into sugary solutions assume another form; they remain short, and increase by sprouting. The bud-forms of the mould are often so like Yeast that they are mistaken for it. Only the parts of a mould which respire and are in contact with the oxygen of the air develop spores, these being usually distributed by currents of air; the parts submerged in a fluid to which the free oxygen of the air has no access do not form spores, but they multiply with incredible rapidity, just like Yeast and bacteria. This multiplication is carried on at the expense of the organic compounds contained in the liquids or succulent bodies attacked by the mould. The changes in the objects attacked are not limited to the acquirement by the mould of as many organic compounds as it requires for food, but the whole mass becomes decomposed and destroyed, and finally is wholly converted into carbon dioxide, water, sulphuretted hydrogen, ammonia, and other volatile substances—a process which has already been described. This decomposition brought about in the absence of oxygen must be termed fermentation. If the fluids and succulent bodies attacked by the moulds contain nitrogenous compounds, they make their presence known by the unpleasant odour they give off when undergoing fermentation, *i.e.* putrefaction. If, on the other hand, non-nitrogenous compounds are fermented by a mould, alcohol may be produced. In sweet, fresh fruit which has been attacked by moulds, the cells of the mould which permeate the succulent tissue produce a fermentation of the juices by which alcohol and ethereal oils first arise as products of decomposition, and by which the characteristic smell of putrescent fruit is produced. It is ascertained that one species of mould, *Aspergillus niger*, when on the surface of a tannin solution, consumes the tannin in the presence of atmospheric air, by which means carbon dioxide is formed. When this same species is submerged in the fluid, and has no free oxygen at disposal, it splits up the tannin completely into glucose and gallic acid. It has also been shown that mould cells which get into the blood of living men and animals cause it to decompose as do bacteria, *i.e.* they produce severe diseases, sometimes ending in death. Many species of mould not only bear the high temperature of the blood without injury, but

even develop very luxuriantly there. The principal genera whose species cause fermentation are *Mucor, Aspergillus, Penicillium, Botrytis,* and *Eurotium.*

Finally, in addition to bacteria, yeasts, and moulds, the mycelia of those fungi, which are called Basidiomycetes (in reference to their characteristic reproduction, which will be described in the next volume), can induce fermentation. The thread-like cell-chains of these mycelia look like mould-structures; they grow through and permeate the dead bodies of plants and animals, dung and refuse, and black meadow-soil, the humus of the forest, and especially the trunks of dead trees. But living plants also, especially the wood of living trees, may be penetrated by these mycelia, and the tree ultimately killed in consequence. When the mycelial threads penetrate into the wood of a living or dead tree (see fig. 32 [3]), they are not satisfied with merely piercing the cell-walls, and destroying those places only with which they come immediately into contact, and absorbing the results of the destruction as food; on the contrary, we have an extensive decomposition, with which is associated a liberation of carbon dioxide, water, and various volatile materials, not well known, which give rise to a peculiar musty smell. The wood loses weight, becomes rotten, and wholly transformed into a mass which on drying crumbles to powder, or into a fibrous asbestos-like substance. Finally, it disintegrates into dust. In popular language this fermentation produced by the mycelium is called "rotting". By many basidiomycetous mycelia the wood is not only changed into a powdery, but even into a liquid mass, as, for example, by the mycelium of the detested Dry-rot, or Wine-cask Fungus.

All these fermentations, whether caused by the mycelia of Basidiomycetes, the bud-forms of mould, by yeast, or by bacteria, have one thing in common, that they have been set up by ferment-causing cells, *i.e.* by the active living protoplasm within them without the excretion of any special chemically-active materials which would come directly into contact with their surroundings. The living protoplasm of the mycelia named, of bacteria, yeast, and mould, itself remains chemically unaltered; it acts most energetically in the immediate neighbourhood, less vigorously further off, and its effect diminishes with increasing distance. The effect proceeding from the ferment-cells might be compared with the concentric waves produced on the surface of water into which a stone has been thrown. A hypothesis has been formulated, according to which the groups of atoms in the ferment-protoplasm are supposed to be oscillating as long as it is alive, and it is imagined that these oscillations are propagated and conveyed to the environment after the manner of a wave-motion. Alterations in the construction of the shaken molecules, displacement of the atoms, and decomposition of the compounds in question, would thus result from the shaking so produced. It has even been estimated that the vibrations which proceed from the living protoplasm of, *e.g.* Yeast cells, are propagated to a distance of $\frac{1}{50}$ mm. from the surface of the cells, and that they shake and alter the arrangement of the molecules of sugar even at this distance. The shaking would of course vary according to the specific constitution of the protoplasm. It may be assumed that vibrations differing in quality

proceed from different fermentative agents, and that consequently diverse decompositions are produced by different bacteria.

This much is certain, that in fermentation, as in respiration, a certain amount of kinetic energy is set free by the living protoplasm and transmitted to the environment, and that in this respect fermentation and respiration behave alike. Thus it also becomes evident that fermentation and respiration can replace and supplant one another. In many moulds, as, for example, in *Mucor racemosus*, this substitution is very noticeable. If the mycelial threads rise up from the liquid, which serves for its substratum, into the air, and if they can draw oxygen from the surrounding atmosphere, then respiration takes place; but if this mould is submerged in the liquid, so that it can no longer obtain free atmospheric oxygen, then the cells become altered, pass into the sprout form, and instead of respiration we observe in them the ferment-action described. Submersion may be regarded as an abnormal condition for these moulds, and perhaps for Yeast also, but for bacteria it is scarcely so, and for them respiration must be regarded rather as the abnormal condition.

I cannot close these speculations without again repeating that fermentation and respiration are only carried on by living protoplasm, that the movements which thus proceed from the protoplasm cease immediately life is extinguished, and that these movements must be assigned to that force of nature acting in the protoplasm for which I claim the old term "vital force".

GROWTH AND CONSTRUCTION OF PLANTS.

1.—THEORY OF GROWTH.

Conditions and Mechanics of Growth.—Influence of Growing Cells on their Environment.

CONDITIONS AND MECHANICS OF GROWTH.

Whoever wishes to germinate seeds must moisten the earth selected as soil, or else must supply water to the seeds in some other way. The seeds absorb the water; the embryo bursts its covering, sends out rootlets into the ground, and its stem and leaves grow up towards the light. The young seedlings must now be diligently watered if they are to flourish and increase in bulk, for they require for their growth an astonishingly large amount of water. Other plant organs which it is desired should grow or be kept in vigorous development are like the seeds, and the suitable watering of cultivated land is, and always has been, one of the fundamental conditions of plant culture. In uncultivated districts the dependence of growth on the water supply appears no less remarkable. Where vegetative activity is brought to a standstill not by the cold of winter, but by heat, the commencement of the rainy season is, each year, the signal for the revival of growth. The amount and duration of the rainfall govern in a most striking way the whole progress of plant development. As soon as the first moisture soaks through the soil, after a long drought, the plants wake up from their lethargy, the dry, sunburnt landscape becomes adorned with vivid green, and the luxuriance of the shoots and leaves arising from the seeds and buds stands in strict proportion to the quantity of water daily supplied to the growing plants.

Why do plants require these quantities of water? The answer to this question has already been partly given in a previous section of this book, when it was shown how the absolutely necessary mineral food-salts were taken up by means of water; how the water in which the food-salts are dissolved is conveyed by root-pressure and by suction to the place of consumption. But this is certainly not the only significance water has for plants, for it would leave unexplained why growing seedlings which cannot yet absorb mineral food from the earth, and which do not even require it, still consume so much water. It must also be remembered that those chemical processes in vegetable cells in which mineral food-salts are worked up do not yet themselves constitute growth, but only a preparation for growth. Mineral salts play an important *rôle* in the transformations going

on in the living cells, and the manifold changes in the production of organic compounds of the food taken in from outside, and in the preparation of these compounds for building materials. But they are not directly concerned in the insertion and fixing of the building materials in the living cell-body, in the further growth of protoplasm, and in the increasing dimensions of the growing cells, which last-named processes alone may be looked upon as growth. Exactly how far water is concerned in growth will be described in the following lines.

Although only very little is known with regard to the minute structure of the protoplasm of the cell, yet this much is beyond question, that it consists of firmer and softer parts, which form an extremely complicated net-work, ever varying in structure from species to species, and with meshes filled with very many different substances, with water, fluid carbohydrates, albuminous compounds, dissolved salts, &c. It may also be imagined that fluid substances can be interpolated in the net-work, resembling it in structure and in consistency at the moment of insertion; that is to say, which receive the same molecular arrangement, and so become an organized portion of the cell-body. The cell-wall also, at the periphery of the protoplasm, must possess a structure which renders it possible that between the already-formed firm portions fluid molecules can be inserted, which then assume the properties of those established portions. This insertion, however, presupposes an extension of the firm parts already present, a separation of the groups of molecules of the organized structures, and a place for the particles to be inserted, and, on the other hand, repelling and attractive forces which control the portions to be introduced.

We are now prepared to admit that here a very important part must be assigned to the *turgidity* of cells. As has been shown, the cell-sap of growing cells is acid, and the acids and acid salts contained in it attract water from their surroundings with considerable energy. The water thus brought into the vacuoles of the protoplasm exercises a strong pressure on the peripheral layer, and indeed on the cell-wall as well as on the protoplasm, which pressure first of all causes an extension of these layers beyond the normal cohesive limit. By the elasticity of the extended layers obviously a pressure is exercised on the fluid in the interior, and this condition of mutual tension is called turgidity. In order to explain the existence of this turgidity, it must be taken for granted that the water conveyed into the vacuoles of the protoplasm by the attraction of the acids and acid salts does not go back again, in spite of the pressure it exercises on the surrounding layers; that it rather is held fast by the molecules of sugar and albumin in the protoplasm. Experience confirms this supposition, and it is evident that water penetrates with great energy from the surroundings into the cells, that the cell swells, the peripheral cell-layers experience a tension, and that yet no water proceeds through them. When protoplasm forces out water in consequence of a stimulation, or when the strained layers are artificially punctured, only then does the fluid come out of the rent formed like a tiny spring. But this again only shows that the fluid in the interior is subject to a strong contra-pressure from the

peripheral layers. This pressure is obviously stronger the more elastic and the firmer are the peripheral layers; and the elastic outermost parietal layer of the cell is of course adapted to exercise an especial reaction on the fluid in the interior of the cell. But that a pressure exists both towards the interior and in the reverse direction, in structures which have no cell-wall and consist only of protoplasm, is shown by the fact that if rents are made in the outermost layer of myxomycetous plasmodia, fluid substances immediately pour out.

It is indeed a matter of course that in a swollen, turgid cell the molecules of the peripheral extended layers will be separated beyond the usual limit of cohesion, and this is near to assuming that in the widened interstices so formed fluid materials are forced which become firm the moment they are deposited, and then resemble in every way the molecules they have driven apart. This intercalation and hardening of constructive materials, which indicates an accompanying increase in the bulk of the organized substances, is to be regarded as growth. We thus obtain a conception of the mechanism of growth, which, though only hypothetical, is in harmony with the external visible phenomena. We are led to it especially by the fact that only cells which are turgid grow, whilst cells stop growing, even although the necessary amount of fluid building material is present, as soon as their turgidity diminishes.

The turgidity of cells, that is, the presence in them of water necessary for their swelling, is, however, only one condition of growth; a second condition, no less important, is *warmth*. Without heat there is no growth. When in the temperate zones, where the year is divided into summer and autumn, winter and spring, the summer draws towards a close, and the days become shorter and shorter, when during the long nights the soil loses more warmth by radiation than it gains during the day, and when, too, plants become very much cooled, growth above-ground entirely ceases, and the whole energy of the plants is concentrated, as we have shown in previous sections, in changing itself into a chrysalis for the winter, in withdrawing from the deciduous foliage the materials which can be employed in the ensuing period of vegetation, and in lodging them in protected store-rooms. During the winter, then, the cooled portions, unprotected against frost, rest, and their growth is completely interrupted. At length winter is past, the last snow has vanished under the breath of mild spring breezes; the hard frozen earth is liberated from the bondage of the frost; everywhere new life stirs, buds swell, trees adorn themselves with flowers and fresh foliage, the meadows become green, seeds germinate, and the crops in the fields spring up vigorously, to the joy of the farmer. On warm, sunny spring days everything grows with astounding rapidity: on cool, dull days the increase is only small. If occasionally a relapse occurs, and the temperature again sinks low, then the growth is wholly arrested. It has been found that the increase of young herbaceous plants on two successive days had sunk in consequence of a sudden storm and visitation of cold from 8 cm. to $\frac{1}{2}$ cm. There is no doubt that such a decrease of growth stands in causal connection with the fall of temperature, and also that quick growth is to be laid to the account of

a rapid increase of heat, provided, of course, that the other factor of growth previously indicated, viz. water, is present in sufficient quantity.

It has been shown in a previous section that the mineral salts, which plants require for the production of building materials, are brought by means of water to the place of need, and that this transporting water is raised from below by evaporation from the surface of organs exposed to the air and sun. This evaporation, however, requires much warmth, and there can be no doubt that the hastened or retarded development of vegetation is partly dependent on quickened or retarded transpiration; that is to say, on the greater or less amount of heat supplied. The conduction of food-salts by means of water from the soil is, however, not by any means growth; it is only a preparatory process, as also is the formation of organic materials in green cells, and the complicated transformations and distribution of materials which follow the elevation of the water from the ground. Warmth is an essential condition of that process which is being here discussed, that is of growth in its narrow sense, as well as of all these preparatory processes.

The part taken by heat in actual growth, that is, in the transformation of fluid building materials into firm, organized portions of the plant-body, and increase of bulk of the cells, cannot be essentially different from that which occurs in other molecular re-arrangements and chemical changes. Heat, according to prevalent theories, is the expression of vibration of ultimate particles. Those vibrations of ether which are known as free heat can induce a corresponding motility of the molecules in any ponderable body. Similarly, heat induces a state of motility amongst the molecules of living protoplasm. We must imagine that work is done upon the organic bodies which constitute the building materials of plants, that they are led in a fluid state to the regions where they are required, and there transformed into solid organized matter. In this way free heat is transformed into latent heat, and in this sense we may regard growth as a consumption of free heat. Accompanying this organizing action of heat there is an insertion of new molecules between the pre-existing ones. The separation of these latter is of course brought about, as already described, by turgidity. Thus, by the co-operation of heat and turgidity, fluid organic materials are changed into firm, solid, organized substances, and in this way the organized portions increase in bulk, in other words, they *grow*.

EFFECTS OF GROWING CELLS ON ENVIRONMENT.

Work is not only performed in the interior of cells, but pressures also come into action which operate on the surroundings with irresistible power. What the cells, apparently so delicate, are able to perform, borders almost on the incredible.

Where the filamentous hyphal threads of crustaceous lichens have penetrated

into the tiny crevices of stone, they crack and crumble the permeated substratum not only by lateral pressure, but they act also lever-wise, and vigorously press up the shattered particles. The absorbent cells or rhizoids of mosses and liverworts also exercise a like action on their substratum, and this is maintained, as in the lichens, essentially by the fact that substances are excreted from the growing cells by which the substratum is partially converted into soluble compounds. Moreover, the pressure which these delicate cells exert on the substratum by their growth may be demonstrated by experiment. If liverworts are laid upon damp folded filter-paper in a space saturated with vapour, in forty-eight hours they will send out rhizoids which grow through the paper. The holes in which the cells of the rhizoids are now seen certainly did not previously exist in the paper. The felt of threads in the filter-paper is so dense that starch-grains of maize, having a diameter of only about 2 thousandths of a millimetre, cannot find sufficient space to slip through, and thus still less can the rhizoids of liverworts penetrate the felt, as these have a diameter of from 10 to 35 thousandths. The holes must, therefore, be first formed by the growing cells of the rhizoids. The threads of the felt must be powerfully driven asunder, and this requires at any rate a comparatively large expenditure of force.

The hyphal threads of a mushroom, which unite to form dense fructifications and grow up from the subterranean mycelium in a comparatively short time, often raise considerable pieces of earth, and the cap-shaped fructifications of *Lactarius scrobiculatus*, *Agaricus vellereus*, and *Hydnum repandum* are indeed frequently thickly covered with larger and smaller fragments of earth, raised by them during their upward growth. An instance is also known in which a stone of 160 kg. was raised and shifted by the growing fructification of a fungus of the mushroom tribe.

Nor is the pressure which the growing cells of flowering plants exert on their environment less considerable. The absorbent cells of roots embedded in the earth, which are called root-hairs, appear fairly straight, although the spaces between the particles of soil filled with air and water are certainly not rectilinear. It cannot be doubted, therefore, that the root-hairs in spite of their delicacy, nevertheless push the small particles of earth on one side, and in their growth follow, as nearly as possible, a straight course. The apices of the main roots of flowering plants, when they grow downwards, form actual channels by pressure on their environment, pushing the portions of soil powerfully asunder, and penetrating into the ground like a gimlet. And it would be a mistake to suppose that they are only drawn downwards by gravity. The roots of bean-seeds which have been germinated in a layer of water spread above quicksilver actually penetrate into the quicksilver. It has often been noticed that the roots of trees which have reached fissures in walls or clefts of rocks are able to shatter the walls and to crack the stone by their further thickening. One at least out of the great number of instances may here be noticed. On either side of the little Tyrolese Gschnitz-thal are terraces strewn with large blocks of stone, which are considered ancient diluvial moraines. The blocks

of stone are composed for the most part of crystalline schist, especially of gneiss, in which mica is arranged in almost parallel streaks. On one of these blocks (represented in fig. 130), at a height of 2 metres, a larch has long ago established itself and rooted firmly, so that the strongest of its roots grow downwards in a cleft parallel to the direction of the mica streaks. By the thickening of this root the crevice became widened; half of the upper block was separated from the lower and was raised about 30 cms. It is estimated that the weight of this raised portion amounts to 1400 kg., and the root which was able to raise this burden exhibits in

Fig. 130.—Elevation of a Block of Stone in consequence of the growth in thickness of a Larch Root.

its thickest part a diameter of only 30 cm. Moreover, the burden overcome by this larch root is small in comparison with that raised by the roots of old trees. The large superficial roots which creep over the ground of the forest like gigantic snakes were not always situated in this position. As long as the trees were young their roots extended under the ground. Only with increasing thickness did these roots, pressing against the firmly compacted earth lying beneath them, become visible above ground, since they burst through the layer of earth situated above them. But with this must also be connected the elevation of the whole trunk with its boughs, which all bear upon the roots, and often weigh several thousand kilogrammes.

It is a matter of course that growing stem-structures also exercise a considerable pressure on their environment. Those underground stems which are called *runners* do not in this respect differ materially from roots, and are similarly able to shift

and press asunder small stones and clumps of earth. In many plants the growing points of the runners are covered with hard scales, which produce exactly the same effect as the points of an auger. This applies especially to several grasses (*e.g. Calamagrostis, Lasiagrostis*, and *Agropyrum*). The runners of the common creeping Couch-grass (*Agropyrum repens*) bore through the roots of trees, and not only through old and rotten but also through young vigorous specimens. The runners of the Couch-grass are often found penetrating through the centre of potato-tubers, and it has been confirmed experimentally that these runners in their growth are capable of even boring through discs of tin-foil. Very instructive also is the penetration of old tree-trunks by the stems of various small shrubs and shrubby trees whose growing points are comparatively delicate and soft in texture, and are not beset, like those of the Couch-grass, with hard pointed scales. Almost everywhere in our mountain regions are to be seen, in places where not very long before a forest has been cleared, dead stumps of fir-trees, rising perhaps a metre above the ground, and overgrown with cranberry and bilberry bushes. The surface where the saw has cut through the huge trunk is partly overgrown with the same plants as those growing in the soil round about, and it has a very peculiar appearance when on these decayed stumps, as if on the platform of the base of a pillar, small colonies of cranberry bushes are seen to flourish luxuriantly—a story higher than on the surrounding ground. Without closer investigation anyone would think that these bushes had germinated from seeds which had previously fallen into the cracks of the stem section, and it is not a little surprising therefore, on splitting such old tree-stumps, to find that this is not the case, but that rather the cranberry bushes of the surrounding forest-ground have sent out their runners into the lower portion of the tree-trunk, and that these have then grown up through the rotten wood of the stump—especially through the decayed part between the wood and bark—until they have again reached the daylight above on the exposed section, showing at any rate that they must have exerted a very considerable pressure on their surroundings. The thin stems, also, of plants growing on boulders have frequently to make a new pathway for themselves when their habitat has been covered by a torrent with sand and stones a span high, and thus have to push out of the way obstacles of comparatively large dimensions. On a forest soil covered with sand and boulders I saw indeed how the delicate thread-like stem of a winter-green (*Pyrola secunda*) had grown up more than 60 cm., and in doing so had pushed on one side stones of a gramme weight. If peas, beans, and other large seeds are buried in the earth and allowed to germinate, it may be seen how by the growth of the seedling small clods of earth and stones are raised, and the earth in which pine-seeds, oats, and beech-nuts have been embedded, looks when the seeds are germinating as if it had been rummaged and thrown up by mice. A fine example of external work done by growing stems must yet be instanced in the growth in height of the forest-trees which we have daily before our eyes, but only too easily overlook on account of its commonness. A young beech trunk 50 cm. thick will raise each year a crown which has a weight of two thousand kilogrammes

through a metre, and in still larger forest-trees the figures become even more impressive.

And all this is accomplished by the invisible atoms of the living protoplasm, which, set in motion by heat, alter their position, attract and repel one another, displace and travel between one another, assume new groupings, and in these new arrangements appear outwardly to our senses in altered form and increased volume.

On glancing over these effects of growing cells and groups of cells, one is reminded involuntarily of the analogous phenomena of ice crystallization. When ice is formed in a glass bottle filled with water, it bursts the vessel with irresistible force, and the splitting of masses of rock in high mountains and in all those regions where the temperature in winter sinks below freezing-point depends in no small degree on the freezing of the water which has penetrated into the smallest crevices and rocky clefts. And yet there is an essential difference between growth and crystallization. Crystals are formed spontaneously from fluid substances, and grow from the depositions of small atoms on their surface. Vegetable cells, on the other hand, never arise spontaneously from fluid materials, but always only by means of an already present organized and living mass of protoplasm. Thus all growth in living things is really only a further development of what already exists. The crystal can again be transformed into a formless fluid mass, can be reconstructed from this fluid, and this alternation may be repeated innumerable times. In plants, on the other hand, the passage from the formed, organized, to the formless, fluid condition is synonymous with death, and from the gases and fluids which are derived from the decomposition of a vegetable-cell a plant-cell never again forms itself spontaneously, that is, without the interposition of a living agent. While, as above remarked, crystals grow by the deposition of small particles on their surface, growth of protoplasm takes place by the interpolation of new molecules between those already present; these are separated from one another, and only subsequently can parts of the cell increase by deposition brought about by living protoplasm.

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2. GROWTH AND HEAT.

Sources of Heat.—Transformation of Light into Heat.—Influence of Heat on the Configuration and Distribution of Plants.—Measures which protect Growing Plants from Loss of Heat.—Freezing and Burning.—Estimation of the Heat necessary for Growth.

SOURCES OF HEAT. TRANSFORMATION OF LIGHT INTO HEAT.

Whence do plants derive the heat necessary for their growth? With regard to this question one may first of all think of that heat which is liberated by the plant itself in respiration, and which can again find employment immediately after its release, not only in metabolism and transport of materials, but also in growth. Further, we may be reminded of that heat which is liberated by the breathing of

animals and in various other instances of slow and quick combustion of organic bodies, which the growing plants can now and then directly utilize. These, however, are only derived sources of heat. Heat which is liberated in respiration is really only the sun's rays which the plants have absorbed on a previous occasion, and ultimately, so far as it comes under consideration for the life of plants, all heat is derived from the sun. The heat which is conducted to plants from the soil, from water, and from air, also takes its origin from the sun, which is therefore to be looked upon as the fountain-head of all the heat utilized by plants.

It has been found that the sun sends out three kinds of rays distinguished by their different periods of vibration, and known respectively as heat rays, light rays, and chemical rays. These three undulating movements of the ether interfere with each other in their course as little as the wave-circles which intersect on the surface of water. We recognize and measure them by their effects. As soon as they strike a body, work is performed by the active force of these ether waves which we picture to ourselves as movements of the molecules and atoms of the body affected; and this work appears either as heat, or light, or chemical change. But it is exceedingly remarkable that only that movement which we regard as heat can produce that transformation of building substances into organized materials, which is, in other words, growth. The vibrations which constitute light, and whose great importance in the formation of the constructive materials, and generally, of organic compounds from inorganic food, has been previously described in detail, are not able to cause such an effect, at least directly. There are even instances which justify the opinion that growth is actually restricted and hindered by light. This much is certain, that growth can proceed in the deepest gloom, if only the two earlier-mentioned factors—turgidity and heat—are undiminished. Seeds and the majority of spores germinate in darkness. The cells of underground stems and scale leaves, those of roots embedded deep under the soil, as well as the mycelia of fungi, grow in regions wholly deprived of light. Moreover, plant organs which are brought from the light into darkness continue to grow there, provided always that the necessary amount of moisture and heat be supplied to them.

Nevertheless very numerous experiments tend to prove that growth can be assisted by light. The following is one of the most remarkable. If plants are cultivated in two places, identical as to the amount of heat affecting them during growth, but differing in the intensity and duration of the flow of light, they will exhibit a quicker growth in the place where the light can act on them more powerfully and for a longer time. Thus plants grow much more quickly in the far north, where they are daily illuminated for twenty hours, than in southern latitudes where they are exposed to the light for only twelve hours, even although in the same space of time comparatively less heat reaches them in their northern habitat. From the small table inserted opposite, giving the commencements of the flowering periods best adapted for the comparison of a definite amount of growth in several widely-distributed plants, at Athens, Vienna, and Christiania, it may be seen that Athens is about forty-six days earlier than Vienna, but Vienna only

Commencement of Flowering.	Athens. 37° 58′ North Lat.	Vienna. 48° 11′ North Lat.	Christiania. 59° 55′ North Lat.
Hepatica (*Hepatica triloba*),...	22nd January	11th March	2nd April
Sloe (*Prunus spinosa*),..........	5th February	18th April	18th May
Gean (*Prunus avium*),..........	1st March	19th April	19th May
Wild Pear (*Pyrus communis*),.	20th March	23rd April	22nd May
Barberry (*Berberis vulgaris*),...	10th April	9th May	6th June
Elder (*Sambucus nigra*),........	15th April	26th May	2nd July
Privet (*Ligustrum vulgare*),....	20th April	4th June	6th July
White Lily (*Lilium candidum*),	1st May	24th June	16th July

about twenty-nine days before Christiania. And yet the difference of the geographical latitude between Athens and Vienna amounts to 10° 13′, and that between Vienna and Christiania to 11° 43′; from which it would be expected that Vienna would have a start of fifty-one days in advance of Christiania.

One is tempted to think at first, in explanation of this phenomenon, that growth depends upon the formation of constructive materials from inorganic food; that this latter process can only be accomplished under the influence of light; and that therefore light so far is important for growth. On the other hand, it is difficult to imagine that the light enjoyed by plants growing in Athens should not be sufficient for the formation of organic compounds in the green cells, and for the production of a sufficient quantity of building materials, since, as a matter of fact, the species in question do not appear in any worse condition in Athens than in Christiania, which, however, it must be supposed would be the case if there were a disparity between the food absorbed, metabolism, and growth. This phenomenon suggests rather that the light in the north is able to take the place of heat. And herein lies also the solution of the problem. Not only is there compensation alone; but the light is changed into heat before it acts on the building materials. A portion of the light falling on the plants is reflected, another portion penetrates into the plants, and of these latter rays part bring about the transformation of carbonic acid into carbohydrates, and increases the store of chemical energy, while another portion is changed into heat. This applies particularly to those light-rays which are most vigorously absorbed by chlorophyll and anthocyanin, and which also cause the fluorescence of these colouring-matters; and among the tasks assigned to chlorophyll and anthocyanin, the transformation of light into heat is certainly not the least important.

But with this we come back once more to anthocyanin—that remarkable colouring-matter which has repeatedly been spoken of in detail. It has been mentioned that anthocyanin frequently occurs only on the under side of foliage-leaves. This is observed especially among plants in the depths of shady forests, which, although belonging to widely-differing families, agree in a remarkable manner in this one point. One group of these plants has thick, almost leathery, evergreen leaves lying on the ground, which arise from subterranean tubers, or root-stocks, or from procumbent stems. The widely-distributed *Cyclamen europæum* may serve as a type of this group. A vertical section of a similar

leaf is given in fig. *r* of Plate I. Amongst other species belonging to this group may be mentioned *Cyclamen repandum* and *C. hederifolium, Cardamine trifolia, Soldanella montana, Hepatica triloba,* and *Saxifraga Geum* and *cuneifolia.* Growing in habitats similar to these are to be met biennial, occasionally perennial, plants which in autumn form a rosette of leaves on their erect stems which survive the winter; these are always coloured violet on the side turned towards the ground, while the leaves which develop in the following warm summer on the elongated flower-stalks usually appear green below. To this group belong, especially, numerous Cruciferæ (*e.g. Peltaria alliacea, Turritis glabra, Arabis brassicæformis*); species of spurge (*e.g. Euphorbia amygdaloides*), bell-flowers (*e.g. Campanula persicifolia*), and hawkweeds (*e.g. Hieracium tenuifolium*). Finally, deciduous shrubs are to be found in the depths and on the margins of forests whose leaves do not survive the winter, but which produce on the stems developing in the summer flat leaves whose under side contains abundant anthocyanin, as, for example, *Senecio nemorensis* and *nebrodensis, Valeriana montana* and *tripteris, Epilobium montanum, Lactuca muralis,* and many others. Amongst non-European species may be noticed many Flowering Rushes, Tradescantias, Begonias, and Cypripediums, as well as the Japanese Saxifrages (*Saxifraga sarmentosa* and *cortusæfolia*), which are coloured deep violet on the lower side of the leaf with anthocyanin, and are only found in shady spots in forests.

Since anthocyanin has been already indicated as one of the means of protecting chlorophyll, the question must first of all be considered as to whether such a relation does not exist in the instances just enumerated. It might even be possible that the violet side of the foliage-leaves now turned earthwards was originally turned towards the incident rays of light, while the leaves were still very young, and that the anthocyanin remains in the position once assumed in consequence of the twisting of the leaves, without being assigned any particular function on that account. Opposed to this idea, however, are the facts that in the majority of the plants cited, anthocyanin is only first developed when the side of the leaf in question has already been turned towards the ground; that in many species the violet side is never turned upwards at any period of development; and especially that in all these plants which grow in the shade, no protection of chlorophyll against an over-abundance of light appears necessary; that, on the contrary, it is important for these shaded growths that the scanty light and heat should be appropriated and utilized to the utmost extent.

We cannot therefore assign to the anthocyanin on the under side of foliage-leaves any protective influence upon chlorophyll. On the other hand, everything goes to show that the anthocyanin developed here absorbs light and changes it into heat. Light which, passing through the leaf, would reach fallen dead and dry foliage, or the ground itself in the depth of the forest, would be wasted and useless there. When absorbed by the anthocyanin and changed into heat, it becomes serviceable to the plants, and can exert a helpful influence on the growth of neighbouring cells, and to a less extent apparently also on the metabolism and

transportations of the substances. In the evergreen leaves of those plants in the depths of the forest which are natives of inclement regions, this advantage is obtained from the layer of anthocyanin developed on the lower leaf-surface, that every sunbeam, even in the cooler seasons, can be utilized to the utmost. It is in harmony with this explanation that foliage-leaves of trees, shrubs, and high bushes which grow a considerable distance above the ground, and have below them other green foliage-leaves, are never violet-coloured on their earthward side, and that in richly-leaved bushes whose lowest leaves lie on the soil, these only are provided with anthocyanin. That portion of the light not turned to account in the highest green leaves, and which is allowed to pass through them, can still be utilized by the lower ones; only that light which would pass through the lowest leaves would be lost to the plants, and therefore we have a violet absorbent layer only on that side which lies on the ground.

That which occurs in plants of the forest shade occurs similarly in those marsh plants whose leaf-like stems or flat, disc-like leaves float on the surface of the water. The green discs of duckweeds (*e.g. Lemna polyrrhiza*), of the Frogbit (*Hydrocharis morsus-ranæ*), of the Villarsia (*Villarsia nymphoides*), of water lilies (*Nymphæa Lotus* and *thermalis*), and of the magnificent *Victoria regia*, are strikingly bi-coloured, being light-green above and deep violet below. Here again it cannot be said that the anthocyanin forms a protection for chlorophyll, but the violet colouring-matter can retain light in the cells on the lower surface of the leaf, and can change it into heat and so make it useful to the plants. The rays which penetrate the green leaf-discs and shine through the water would otherwise be lost to the plants in question, for none of the species enumerated have submerged leaves, but possess only these floating discs, green on the upper and violet on the lower side.

If anthocyanin were found, not only on the under but also on the upper side of the foliage-leaves, then indeed the significance would primarily be assigned to it of a means of protection for chlorophyll, and of assisting the metabolism and transport of materials; but obviously the blue colouring-matter would not, on the upper side of the leaf, behave essentially otherwise as regards its capacity of changing light into heat, than on the lower side. It is even probable that the importance of anthocyanin lies, not only in its retention of the rays injurious to metabolism, but also in the transformation of light waves into heat. In support of this view there is at least the fact that anthocyanin is also richly deposited on the upper side of the foliage-leaves at times when, and in places where, other sources of heat are deficient, and that generally leaves and stems of many plants growing in such places are entirely overspread with red or violet. A number of small annuals which grow very early in the spring at a low temperature (*e.g. Saxifraga tridactylites, Hutchinsia petræa, Veronica præcox,* and *Androsace maxima*) are usually coloured with anthocyanin on all sides of their growing organs. Moreover, seedlings which spring up from the earth at low temperatures, and above all high Alpine forms in the neighbourhood of the snow-line, are abundantly

provided with anthocyanin on both leaf-surfaces. The leaflets and stem of the Alpine *Sedum atratum*, those of *Bartsia alpina*, and, above all, numerous species of *Pedicularis* (*e.g. Pedicularis incarnata, rostrata, recutita*) are coloured wholly purple or dark violet, and this in habitats where the colouring could not possibly be regarded as a protection for chlorophyll. It is also a very striking phenomenon that widely-distributed grasses (*e.g. Aira cæspitosa, Briza media, Festuca nigrescens, Milium effusum, Poa annua* and *nemoralis*), which in the valley possess pale-green glumes, develop anthocyanin in them on lofty mountains, so that there the spikes and panicles exhibit a deep violet tint, and on this account the regions in which grasses of this kind grow in great quantities receive a peculiar dark colouring. Indeed, this tint becomes the more intense the nearer the habitat of the plants in question is to the snow-line, and the more intense the action of the sunlight becomes. In this case anthocyanin can certainly not be looked upon as a means of protecting chlorophyll, as the glumes generally contain but little of that substance, and take so little part in the formation of organic materials, that the few chlorophyll-grains might be entirely absent without the plant suffering any damage. On the other hand, it may be supposed that the intense light of the elevated region is changed into heat by the abundant anthocyanin of these glumes, that this heat reaches the germs hidden under the glumes, and there favourably influences the growth of the seeds as well as the transformations of materials. The same occurs in the numerous sedges and rushes growing in the Alps, which have dark-violet, almost black, scales covering the flowers (*e.g. Carex nigra, atrata, aterrima, Juncus Jacquinii, trifidus, castaneus*), and probably some of the varieties of tint observed in the corollas of Alpine plants are also to be explained in the manner indicated.

It is known that the floral-leaves of many plants growing on lofty mountains, and in the far north, are coloured blue or red by anthocyanin, whilst in the same species, growing in the warm lowlands and in southern districts, they appear white. Particularly noticeable in this respect are the Gypsophyllas (*Gypsophylla repens*), the Carline Thistle (*Carlina acaulis*), the large-flowered Bitter-cress (*Cardamine amara*), the Milfoil (*Achillea Millefolium*), and many of those Umbelliferæ which have a very wide distribution, and occur all the way from the lowlands up to a height of 2500 metres in the Alps, such as; *Pimpinella magna, Libanotis montana, Chærophyllum Cicutaria*, and *Laserpitium latifolium*. Since it has been proved that the colours of flowers are eminently important as a means of attracting insects, it might be thought that the above cases are in some way connected with insect-visits. Without wishing altogether to deny such a relation, the possibility, on the other hand, must not be excluded that anthocyanin plays the same part here in the flowers as in the glumes of grasses, and in the clothing scales of sedges and rushes; and that in the cold Alpine regions, that which is deficient in the amount of heat directly absorbed as such, is compensated for by such as is obtained from light-rays by means of anthocyanin. In support of this view there is also the phenomenon that many plants which develop white flowers in the warm

summer, as, for example, *Lamium album*, produce late in the autumn, under a very low temperature (if they bloom a second time), corollas whose upper side is tinged with red; and that in the winter, and in frosty habitats, the ray-florets also of many Compositæ, as, for example, of the well-known Daisy (*Bellis perennis*), are coloured red on that side which is turned towards the sky when the capitulum is closed, and towards the ground when the capitulum is open.

INFLUENCE OF HEAT ON THE CONFIGURATION AND DISTRIBUTION OF PLANTS.

On high mountains near the snow-line, and generally in all those districts where the heat supplied to the plants is extremely scant, there occurs, together with a production of anthocyanin, a dwarf and tufted habit. Usually this phenomenon is explained by the large amount of snow, which must have a great effect in these frosty heights during the long winter, and it is believed that high Alpine plants are protected by this form and position of their stems and leaves from injury by the pressure of snow. It cannot indeed be denied that the pressure of the snow has some influence on the form and direction of the stem-structures, and this influence will be explained fully in the following pages in a particularly instructive example, viz. in the mountain pines. But this nestling on the ground of plants growing in the high Alps can only be partially referred to this cause.

It is a mistake to suppose that the annual snow-fall increases with the height. The amount of snow which falls attains a maximum at about 2500 metres above the sea-level. This height marks only the upper limit of mountain pines, dwarf junipers, alders, and rhododendrons. Above this the fall diminishes, and at a height of 3000 metres the snow is no deeper than far down in the valleys. Even where the maximum fall occurs trees are still met with; there are yet larches and Arolla pines, which, on account of the great elasticity of their branches and the downward direction of their older boughs, can bear very heavy weights of snow without becoming broken or crushed. The willows of mountain regions, characterized by the way in which their elongated stems and branches are pressed to the earth (*Salix serpyllifolia, S. retusa, Jacquiniana, reticulata*), and which are represented in fig. 131, grow, however, far above the tree limit, at a height above the sea where the depth of snow, already beginning to diminish, is in no case greater than in the valleys, where Purple and Sweet Willows, and other species of large-leaved willows raise their straight stems several metres high above the ground on the banks of streams. It must also be remembered that the woody growths close to the ground in high Alpine regions are very often established on steep places, where the snow could not easily lie, could in no instance be deeply piled up, and could not exert a pressure on the stems and branches. The delicate Thyme-leaved Willow (*Salix serpyllifolia*) nestles with an especial predilection to the surfaces of rocks, and covers them with an actual carpet, and the Buckthorn (*Rhamnus pumila*) is found exclusively on steep declivities, where it roots in the crevices of the narrow

rock gulleys, and growing out from them overspreads like ivy the vertical rock-faces.

In all these cases it is certain that the weight of snow cannot have any determining influence upon the form of the plants, and some other explanation must be sought. May it not be perhaps that strong winds render it impossible for woody

Fig. 131.—Alpine Willows with stems and branches clinging to the ground in the Tyrol.

plants with erect stems to grow in high Alpine regions? Observing the mist and volumes of clouds rushing across the tops of the mountains, one gets some idea of the strength of the air currents which operate there, and whoever has experienced the effects of a storm on a high mountain ridge can estimate the force of the powerful gusts of wind. And yet it would be erroneous to suppose that the force of the storms on lofty mountain heights is greater than in mere hill regions. In the case of many winds it is even certain that they increase in violence as they rush down

from the mountain ridge deeper into the valley. The Föhn-wind in the Alps often appears on the heights as only a slight breeze, but accelerates its velocity as it enters the valley, and when it arrives there may be as destructive as a hurricane. Therefore if the woody plants on the slopes of high mountains were unable to exhibit erect growth on account of storms, then the neighbouring valleys must also be deprived of upright trees, which, however, is known not to be the case.

The clinging of woody plants to the ground in high Alpine regions must not be regarded either as an adaptation to snow pressure or to storms; it is due rather to the fact that in the high Alps the ground is relatively much warmer than the air, and that plants lying on the soil profit by this higher temperature. I have ascertained through numerous observations at different heights in the Central Tyrolese Alps that the mean temperature of the soil exceeds that of the air by the following amounts:—

At a height of	1000	metres, about	1·5° C.
„	1300	„	1·7° C.
„	1600	„	2·4° C.
„	1900	„	3·0° C.
„	2200	„	3·6° C.

Thus the soil, in comparison with the air, becomes warmer the higher one ascends the mountain. Everywhere the earth absorbs the sun's rays to a much greater degree than the air does; but that the excess of the heat of the soil above that of the air increases so remarkably with the increasing altitude, is due to the fact that the intensity of the sun's rays increases as we ascend.

This is further explained by the fact that the layers of air which absorb the sun's rays are less dense the greater the elevation above the sea-level, or, to use a current expression, that the air is thinner on the heights than in the valleys. As is well known, the water vapour of the air also absorbs the sun's rays, and since this aqueous vapour diminishes rapidly with the height, as might be concluded from the lessening of the pressure, the intensity of the sun's rays consequently increases with the increasing altitude. It has been estimated that the force of the sun's rays on the top of Mont Blanc (4810 metres) is 26 per cent greater than at the level of Paris, and that at an altitude of 2600 metres the chemical activity of the sun's rays is 11 per cent greater than at the sea-level. Everything which is benefited by the sun has, in consequence, a relatively striking appearance in the higher regions of the mountains, and the illuminated soil especially exhibits a temperature of surprising height. On the Pic du Midi in the Pyrenees (2885 metres) the temperature of the illuminated soil rose on a clear September day to 33·8° C., while the air only registered 10·1° C., and in point of fact the temperature of the soil on this summit was almost twice as great as at the Bagnères situated 2326 metres below. On the Diavolezza (Switzerland) the black bulb thermometer registered 59·5° in the sun, and at the same time in the shade a temperature of 6·0°. In the Himalayas the blackened thermometer at a height of over 3000 metres showed in the sun 40°–50° above the temperature of the shade, and once stood at 55·5° while the temperature on the snow, in the shade close by, amounted to only —5·6°. In Leh (Kashmir) at

3517 metres, a blackened thermometer in vacuo rose to even 101·7°, that is almost 14° higher than the boiling point of water, which at that height is only 88° C.

It is readily intelligible that under such conditions growing plants which require heat should nestle to the ground in high mountain regions, or more correctly, that only such plants are capable of living at these heights which make the best possible use of the most abundant of all sources of heat; which, so to speak, seek a warm situation and settle themselves against the sunny stones and the black humus, occupying and covering the rocky crevices. Plants whose nature is to grow erect with their woody stems in the air would not succeed well in Alpine regions, and ultimately would be crowded out by species which thrive better by clinging to the relatively warm soil.

The increase in the excess of the ground temperature above that of the air with the increasing altitude is also manifested in another phenomenon which, though it has been frequently observed and discussed, has not always been correctly interpreted. The Ling (*Calluna vulgaris*), which extends from the lowlands at the foot of the Alps up to high Alpine regions, blossoms on the sea-coast in Istria usually at the end of July; in Alpine valleys, which lie 1000 metres above the sea-level, it opens its first flowers at the end of August, and therefore the retardation of flowering at 1000 metres amounts to something over a month. From this it might be expected that the Ling would first blossom at an altitude of 2000 metres at the end of September, but this is not so, for on mountains of the Central Alps at 2000 metres the Ling nestling on the ground is seen to be in full bloom before the middle of September. By comparing the time of blossoming of high Alpine plants cultivated in the botanic gardens at Innsbruck, with the time at which the same species open their flowers at various altitudes on the neighbouring mountains, it was shown that the retardation of the blossoming amounted to a mean of 25 days at an altitude of 500–1000 metres; an average of 18 days at 1500–2000 metres; and 14 days at 2500–3000 metres; and this can only be explained by the much greater intensity of the sun's rays in the high regions, and the consequent elevation of the temperature of the ground above that of the air. It must yet be mentioned, for the completion of the observations here detailed, that all plants in the valleys develop larger leaves and taller stems than those on lofty mountain sites. While the Ling forms considerable bushes with erect branches on the coast of Istria, plants of the same species on the slopes of high mountains 2000 metres above the sea, appear as dwarf shrubs, whose woody stems lie on the ground and are partially imbedded in the dark humus.

The great contrast which vegetation on a mountain exhibits in different parts of the world may be explained by the action of the sun's rays. On slopes illuminated directly by the sun, the temperature of the soil, and indirectly that of the layer of air in contact with it, rises far higher than on shady declivities, and in consequence of this very remarkable differences may occur even in the closest proximity. Observations of the temperature of the soil at a depth of 80 centimetres, spread over

three years, at Innsbruck in the Tyrol, and in the eight points of the compass round an isolated conical sand-hill, have shown the following mean temperatures:—

North.	North-east.	East.	South-east.	South.	South-west.	West.	North-west.
15·3°.	17·0°.	18·7°.	20·0°.	19·3°.	18·3°.	18·5°.	15·0°.

The difference between the south-east and north-west amounts, according to this, to not less than 5°, and it is probable that at higher altitudes it would show even a more marked increase. And herewith is connected the rising and falling of the upper limit of vegetation on the different sides of a mountain. On slopes long exposed to the sun the plants advance much further upwards than on the shaded sides of a mountain, or those which are warmed by the sun's rays during only a short time; and the difference of the upper limit on the north and south sides oscillates in high mountain regions between 200 and 300 metres. It frequently happens that species reach their upper limit on the north side at 2000 metres, while on the south side not until 2400 metres is reached. From this it strikes us that the contrast between the upper limit of plants on the north and south sides becomes greater the higher we climb up into the mountain. In this respect a comparison of beeches and firs is very interesting. Beech trees (*Fagus sylvatica*) find their upper limit in the Limestone Alps of the North Tyrol on an average at an altitude of 1430 metres; on the sunny side of the mountains the beech limit rises to 149 metres above this average, while on the shady side it falls short of the average by 112 metres; thus the difference between the sunny and shady side for beeches amounts to 261 metres. Norway spruces (*Abies excelsa*) find their upper limit in the same region, on an average, at an altitude of 1777 metres; on the sunny side of the mountain the spruce limit rises to 185 metres over, while on the shady side it remains 125 metres below the average, and thus the difference between the sunny and shady side amounts for spruce to 310 metres. Thus whilst in the zone stretching from 1300–1600 metres, the difference between the shady and sunny sides amounts only to 261 metres, it rises to 310 metres in a zone from 1600–1900 metres, which again can only be accounted for by the rising intensity of the sun's rays with the increasing altitude.

From all this it may be seen how vegetation adapts itself to the given heat conditions; how the smallest advantage offered in any spot is made use of; and how much the form of the plant depends upon the conditions of warmth in the habitat.

The above statements also demonstrate that the distribution of plants on the earth stands in the closest connection with the distribution of heat. In another volume of this work an opportunity will be taken of discussing this connection fully; here it is sufficient to mention that from the local conditions of warmth, viz., from the elevation of the temperature of the soil effected in circumscribed spots in mountainous districts by the sun's rays, the preservation of colonies of plants, from earlier, warmer periods is explained. The largest part of the central European uplands, especially the Northern Limestone Alps, exhibit colonies of plant-species on limited areas, which are entirely absent in the immediate neighbourhood, and

which now no longer spread beyond the narrow circle of their confined habitat, although they ripen seeds capable of germinating, and are met with again in great quantities one or two degrees farther south. We may conclude that these plants were first brought to their isolated habitats within the historical period by wind or other distributive agents, and everything tends to show that they represent the remnant of a vegetation which was distributed very widely over adjacent districts in ages long past, but have withdrawn thence in consequence of the severe climate which has intervened; that is to say, have died and been replaced by other vegetation. That such foundlings on isolated mountain slopes, often only a small steep ravine, or on a single rocky face, could maintain themselves even in the later cold periods, is explained by the fact that conditions of warmth can prevail over very restricted areas on the mountains which differ *in toto* from those of the environment, and are only found generally prevailing quite a degree further south. The southern slope of the Solstein range, between Hall and Zirl, produces in limited areas Hop-hornbeams and Bladder-senna (*Ostrya carpinifolia* and *Colutea arborescens*); from the boulders an umbellifer, the curious *Tommasinia verticillaris*, rises to the height of a man; the rock terraces are overgrown with *Stipa pennata*, *Lasiagrostis Calamagrostis*, *Saponaria ocymoides*, *Dorycnium decumbens*, and here and there one might imagine one's self a degree further south on the other side of the Alps. It is beyond question that the plant forms named on the warmest and most protected of the Solstein range are remnants from a primeval warmer period, and were formerly distributed generally over the adjoining mountain ranges. These cursory remarks should show that the accurate knowledge of the relation of heat to individual species of plants may render important help in speculations about the history of our vegetation.

MEASURES FOR PROTECTING GROWING PLANTS FROM LOSS OF HEAT.

Since certain developments in plants have assigned to them the task of utilizing external circumstances as far as possible so that heat may reach the growing organs to the extent actually necessary, it is naturally to be expected that contrivances will not be wanting to protect them from an excess of heat, and also that care will be taken that the heat once obtained is not again lost. It would not be in harmony with what we know of the economy of vegetation that a plant exposed to the sun should lose by radiation in the following night all the heat which it had gained during the day. It is known that growth is carried on during the night, and, indeed, that certain organs grow more in the night than in the day, and in these an excessive loss of heat would be most disadvantageous.

As a matter of fact arrangements exist for protecting plants from an excessive loss of heat. These contrivances coincide in great part with those which regulate transpiration, and have already been fully described in the discussion on that subject, to which therefore we may refer. But those developments which claim a particular interest as measures of protection against the danger of excessive loss

of heat which are not at all connected with transpiration, or only to a slight degree, are brought together here in the form of a general sketch.

First of all in this respect are to be considered flowers of comparatively rapid growth, whose parts therefore require much warmth, but for which many of the contrivances suited to foliage-leaves are not well adapted as protective measures against loss of heat, since other functions might be encroached upon. And yet these flowers especially require an abundant protection against loss of heat, even more than other plants on account of their great sensitiveness. If in the spring a blossoming snowdrop, having already penetrated the soil, is surprised by a frost, the flower-stalk and the leaves sink down as if withered, while the flowers outwardly are not at all altered. Anyone observing this might think that the green stem and leaves had been injured, but that the flowers, on the contrary, had survived the catastrophe without harm. But exactly the opposite is the case. The stem and leaves become erect with returning warmth and continue to grow, but the pollen in the anthers of the flower is dead; also the ovules, styles, and stigmas are affected so that they wither and shrivel up: obviously the production of ripe seeds is then out of the question. It is also observed that the pollen in the anthers is best formed when the flower-buds in question are warmed through by the sun, and when the blossoming plants grow on a free open space which the sun's rays can reach. Moreover, the floral envelopes develop much better in such spots than in cool shady places; they become larger, exhibit brighter colours, and consequently are more often visited by insects than those which receive relatively little light and heat. But the danger that the flowers and flower-buds will again lose by radiation, through the night, the heat which they have gained during the day is most likely to be felt in open, unshaded habitats, that in consequence of the great loss of heat the formation of the pollen in the yet closed anthers will be injured, and finally, that the petals will also be disturbed in their growth and function. In order to avoid this, in many cases the flower-buds and also the open flowers are pendulous, bell-shaped, and tubular, or leaves become arched in the shape of a dome, cap, or umbrella above the stamens and pistils, in which case the inner portions of such flowers are hidden as in a niche or groove. In these hidden nooks they are comparatively well-protected against loss of heat, and at least no radiation of warmth towards the night sky proceeds from the anthers and stigmas. Only the coverings spread over the stamens and pistil, as a protecting roof, lose during the night a great part of the heat obtained in the day. These, however, are not so much endangered, since they have already obtained their normal size and have no need of heat for further growth; besides, they are usually clothed with air-containing, hairy structures, surrounded by dry membraneous edges or entirely transformed into dry parchment or paper-like scales, in which case they can suffer no further damage from loss of heat. The air in the pendulous bell-flowers is 1–2 degrees warmer, in the morning before sunrise, than the surrounding air; here, closed in, it remains practically unaltered during the night; and this of course is exceedingly useful to the warmth-loving anthers and stigmas there hidden.

In many instances the flower-buds and young flowers only assume an inverted position periodically, *i.e.* only when a cold night is to be expected. Many umbelliferous plants are particularly noticeable in this respect, especially *Falcaria Rivini* and the Burnet Saxifrage (*e.g. Pimpinella magna,* and *saxifraga*) and Carrot (*e.g. Daucus Carota* and *maximus*). The sun has scarcely set when in all these species the stalks which bear young flower-umbels bend downwards, crook-like, so that the flower-buds, which during the day have been turned towards the sun, now face the earth, and the finely-divided involucral leaves spread out like an umbrella over the nodding umbel. These finely-divided coverings radiate out heat in the night without injury; the flower-buds below them, on the other hand, are protected in the manner described against the nocturnal radiation so fatal to them; whilst the heat they absorb during the day is thus in great measure, if not entirely, retained. With the next sunrise the young umbels rapidly become erect; their bent stalks rise up stiffly; and the flower-buds are again exposed to the sun, as may be seen in the illustration of the Common Carrot (*Daucus Carota*) inserted opposite (Fig. 132 [1, 2]). Later, when fertilization has taken place, and the young fruits are developing, the necessity for protecting the stamens and pistils from radiation no longer exists, and the periodic bending down of the umbel is discontinued. Young flower-heads of several scabiouses (*e.g. Scabiosa lucida* and *Columbaria*) behave like the umbelliferous plants named, as also do the single flowers of pansies (*Viola tricolor*), represented in fig. 132 [3, 4,] in day and night position next the umbels of the carrot. In numerous Compositæ, Labiatæ, and plantains (*e.g. Leontodon hastilis, Mentha sylvestris, Plantago media, recurvata* and *maritima*) there are no such regular periodic movements; in these the capitula and spikes are always pendulous while the flowers are still in bud, and they remain in this position as long as it is advantageous to them. Afterwards, when the nocturnal loss of heat can no longer be injurious to the anthers and stigmas, or if other protective measures have been developed meanwhile, the axis of the inflorescence becomes stiffly erect. In many Compositæ the involucres of the capitula or the peripheral ligulate florets, and in other families the sepals and petals, bend up after sunset over the stamens and pistils. They thus form a protecting roof under which the temperature of the air alters comparatively slowly, and the delicate anthers and stigmas are secured from radiation.

A very striking contrivance for protecting against loss of heat by nocturnal radiation is also observed in the seedlings of flowering plants, in those which possess two seed-leaves or cotyledons. As long as the embryo surrounded by protecting coats remains quiescent in the seed, the two seed-leaves are situated with their upper surfaces in contact; later, when germination has taken place, when the radicle has penetrated into the earth and the seed-coat is thrown off, the two seed-leaves become separated, turn their upper sides towards the sky, so that the seedling above-ground resembles an open book. In this position the broad surfaces are exposed to the sun's rays; they are also illuminated and warmed as much as possible, and if they are coloured green, the formation of organic

substances from inorganic food can be carried on in them. These cotyledons are frequently seen to increase in extent, and to grow and function exactly like foliage-leaves. It would certainly be a great disadvantage to green cotyledons of this kind if they were obliged to give up either partially or perhaps entirely in the following night the heat received during the day. In neighbourhoods where the greater part of the seeds germinate at a low temperature, at the close of winter at a time when the nights are still long, warmth must be economized as far as practicable, and especially must the loss of heat from the cotyledons by nocturnal

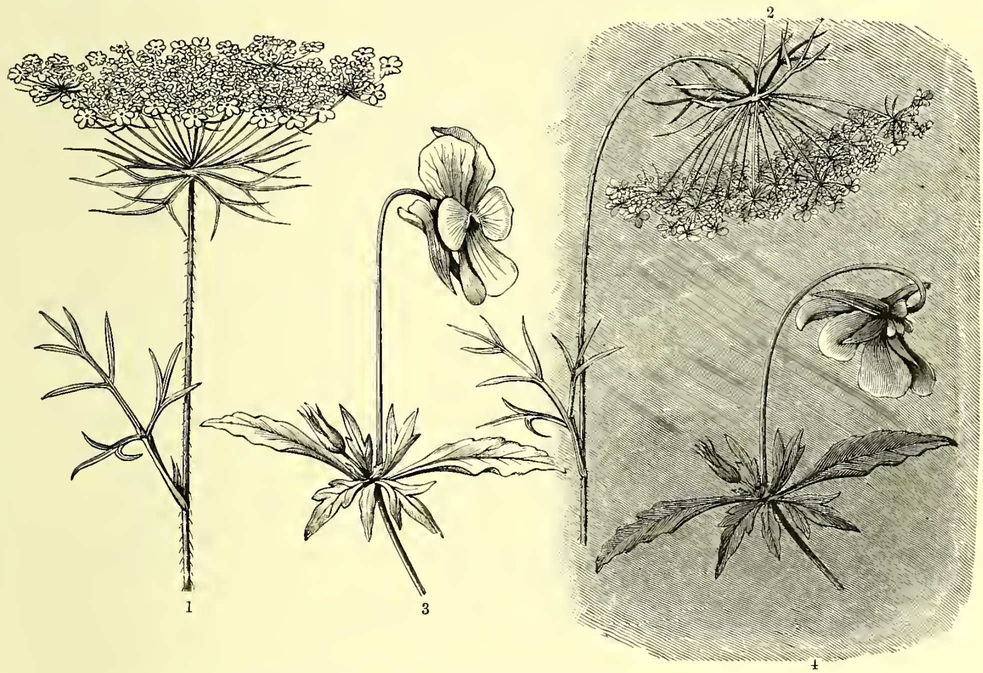

Fig. 132.—Periodic bending of Flowers and Inflorescences.

1 The umbel of the Carrot, day position. 2 The same umbel, night position. 3 Flower of Pansy, day position. 4 The same flower, night position.

radiation be prevented. This is accomplished by the cotyledons, which are separated from one another like the leaves of a book, and whose broad surfaces are turned towards the sky, closing together when the sun sets, and again assuming that position which they occupied in the quiescent seed. In this way the two cotyledons now have their narrow edges turned skywards, and the loss of heat in the night is as much as possible minimized. This movement of the cotyledons, which on cloudless evenings and in exposed spaces occurs more quickly than under cloudy skies and in places which are overshaded by trees, has also the advantage that the small foliage-leaves, which are visible on the rudiments of the shoot between the cotyledons, are covered over through the night. When the morning breaks, and the danger of excessive loss of heat is passed, the cotyledons again open out in order to sun themselves afresh to their full.

This opening and closing of the cotyledons is seen particularly well in species of clover and Bird's-foot Trefoil (*Trifolium* and *Lotus*), in all mimosas and bauhinias, and numerous other leguminous plants; also in species of wood sorrel (*e.g. Oxalis Valdiviana, rosea, sensitiva*), in the gourds, cucumbers, and melons, in the Sunflower (*Helianthus annuus*) and in the Tomato (*Solanum Lycopersicum*), in species of *Mimulus* and *Mirabilis*, the Corn-cockle (*Agrostemma Githago*), the Chickweed (*Stellaria media*), and many others.

By alterations of position, similar to those exhibited by cotyledons, the so-called *compound leaves* are also in many instances protected against nocturnal radiation. By compound leaves are understood those which bear either pinnate or radiating leaflets on a common stalk.

These compound leaves in some cases, which have already been alluded to, are spread out during the mild night, but are, on the contrary, folded together under the burning noonday sun. In by far the greater number of cases, however, especially in species whose habitat is exposed to great cooling in the night, the reverse is observed. In sunshine the surfaces of the leaflets are arranged more or less parallel to the ground, the upper side is turned to the sky, and is fully and completely flooded by the sun's rays. If this position were retained after sunset, the surfaces of the leaflets would be forced to give up much heat by radiation towards the night sky. In order to avoid this the leaflets fold together either upwards or downwards, and place themselves, so to speak, on edge. In this way their broad sides become vertical, in which position they are protected from radiation as much as possible.

There are provided for the accomplishment of these movements certain swollen cushions of succulent tissue at the bases of the several leaflets, and often at the base of the common petiole. These are known as *pulvini* and each consists of parenchymatous thin-walled cells surrounding a strand of compressed vascular bundles, which further up becomes the midrib of the leaflet, which is inserted on the pulvinus. The parts of this strand where surrounded by the pulvinus are supple and very flexible, but above the pulvinus they become stiff and firm, forming as it were the main support of the whole leaflet, so that indeed alterations of position of the midrib are participated in by the whole.

In order to represent clearly how a movement is brought about in the leaflet by means of its supporting pulvinus, let us imagine a straight rod which is only flexible at the base, and is there held fast between two springs. The pressures proceeding from the two springs is equally strong, and the rod is therefore maintained in an upright position. If the pressure of the spring relaxes on one side, the stick must bend over in the direction of the diminished pressure. If the pressure of the two springs be afterwards equalized, the rod will again assume its original erect position. If for the rod we now substitute a leaflet traversed by a rod-like midrib, *i.e.* by the vascular bundle-strand mentioned above, and imagine two opposed halves of a turgid cell-tissue instead of the two springs, then the leaflet will be kept upright by the equal tension of the pulvinus situated at the base of the strand; but as soon

as the turgidity of the cells increases in one of the halves of the pulvinus, in consequence of an increased afflux of water, this half elongates, bulges out, becomes convex, and exerts a stronger pressure than the opposite half, so that the latter becomes concave and much contracted. The supple portion of the bundle-strand between the two halves of the cushion becomes bent, and the leaflet, whose stiff

Fig. 133.—Alteration of Position of Leaflets in Compound Leaves.

[1] Leaf of *Mimosa Lindheimeri*, seen from above, in day position. [2] The same in night position. [3] Leaf of *Amorpha fruticosa* in day position. [4] The same in night position. [5] Leaf of *Coronilla varia* in day position. [6] The same in night position. [7] Leaf of *Tetragonolobus siliquosus* in day position. [8] The same in night position.

midrib is formed by the continuation of the bent bundle-strand, is inclined over in the direction of the concave half of the pulvinus. If the increase of turgidity occurs alternately first in the one and then in the other half of the pulvinus, the leaflet will also be bent now to the one, then to the other side; and if the leaf-support has a horizontal position, an alternate rising and sinking of the leaflet will occur. It is to be noticed here that the leaflet itself remains actually quite passive, and that the pressures which have come into play only operate in the pulvinus.

The commonest stimulation to periodic alteration of the turgidity in the pulvini

is the diminution of light and heat after sunset, and since the rising and sinking of the leaflets effected thereby coincides with the nocturnal sleep of birds and other animals, the phenomenon described has been interpreted in this sense, and termed the *sleep of plants.*

The rapidity with which the movement of the leaflets is accomplished varies very much in different plants, and even in the same species is sometimes quicker, sometimes slower, according to external influences. All the circumstances which increase the turgidity of vegetable-cells have also an accelerating effect on these movements. It is still an unsolved problem how far light and darkness influence the turgidity of the pulvini. It is supposed that the darkening produces an increased afflux of water and an increase of turgidity in the whole pulvinus, but more rapidly in one half than in the other; while the protoplasm in one half of the cells of the pulvinus is stimulated by light to give up a portion of the watery sap, lying at the time within the sphere of its influence, to the surroundings—by which indeed not very much is explained.

In one section of plants whose leaflets assume a sleep position when darkness sets in after sunset, the leaflets provided at the base with pulvini move upwards, and in the other section downwards. The movement is upwards as a rule in ternate leaves, of which the clover may serve as a type. When the elevation has been accomplished, the leaflets are directed either all three almost at a right angle to the horizon, or the terminal leaflet is bent up rather more than the two lateral ones. A very pretty example of this is furnished by *Tetragonolobus siliquosus*, represented in figs. 133 [7] and 133 [8], and also by *Desmodium penduliflorum* as well as by various species of *Lotus, Trifolium, Melilotus, Medicago.* Pinnate leaves, whose leaflets rise up and arrange themselves next one another like the leaves of a closed book, are found on numerous small scrubby mimosa bushes of Peru, of which a species, viz. *Mimosa Lindheimeri* is represented in figs. 133 [1] and 133 [2], in the day and night positions. In the Australian *Acacia lophantha* and several other true acacias, in *Schrankia aculeata* and species of *Æschynomene,* in the American gleditschias, further in the Australian *Clianthus Dampieri* and in the widespread European *Coronilla varia.* In fig. 133 [6] is shown how the erect leaflets of the *Coronilla* lie against one another very regularly in pairs. Just as often, instances are observed in which the leaflets of the pinnate or digitate leaves fall downwards after sunset. An example of this group is afforded by the leaf of one of numerous American amorphas (*Amorpha fruticosa*), which is illustrated in figs. 133 [3] and 133 [4]. These leaflets which droop at night are also very noticeable in the Indian *Averrhoa Carambola,* in various species of indigo and liquorice (*Indigofera* and *Glycyrrhiza*), in the sophoras (*e.g. Sophora alopecuroides*), in the American tree, *Gymnocladus Canadensis,* and in robinias, of which *Robinia Pseudacacia* (popularly called acacia) is planted everywhere as a decorative tree. In like manner in the widely-spread common Wood Sorrel (*Oxalis Acetosella*), *cf.* fig. 90 [8], in the Indian pinnate-leaved *Oxalis sensitiva,* and in numerous American sorrels.

With respect to the radiation, it is immaterial whether the leaflets rise up or

sink down; the main point is that they turn their profile towards the night sky, and this occurs in all the above-mentioned cases. But it should be noticed here that besides the protection against excessive loss of heat, other advantages are gained by the periodic alteration of the position of the leaflets, and in this respect it is anything but a matter of indifference whether the leaflets fold together above or below. Since the vertical position of the leaf-surfaces also furnishes an important protection against excessive transpiration, various conditions of the leaf construction connected with this protection are also significant. For example, the question whether the stomata are developed on the upper or under side of the leaflet is determined, inasmuch as the sides provided with stomata, as a rule, come in contact with one another. Finally, it must nct be denied that bedewing also has an influence on the alteration of position of the delicate leaflet.

A great number of plants whose leaflets assume the sleep position at nightfall also exhibit this phenomenon on bright days when shaken or touched, and indeed more rapidly under these circumstances than at the on-coming of darkness. The slightest touch of the finger, even shaking by a moderate wind, suffices to cause the leaflets of these plants to fold together. In the *Oxalis sensitiva* of tropical India even the disturbances of the air caused by the approach of man is enough to cause the pinnate leaflets to fall together rapidly, and the same thing occurs in several papilionaceous plants (*e.g. Smithia sensitiva* and *Æschynomene Indica*), as well as in several mimosas. When we move away from the immediate vicinity of these plants, and complete stillness once more reigns in the air, the folded leaflets again spread out and turn their upper surfaces skyward. The phenomenon that the plants close up, frightened at the approach of man, as if they felt or in some way became aware of his approach, caused the older botanists to name them *Sensitive Plants*.

From a cursory examination it appears that the folding of the leaflets in these sensitive plants caused by shaking, and the assumption of the sleep position at the setting in of darkness, are the same processes; but closer investigation shows that there is an essential difference between them. Outwardly this difference is recognizable by the fact that in the sleep position, brought about by darkness, the pulvinus below a leaflet remains quite rigid, while in the folding of the leaflets produced by shaking a relaxation of one half of the pulvinus occurs. In sections through the pulvinus of sensitive plants, it is seen that numerous intercellular spaces are contained in that portion of the parenchyma which adjoins the flexible strand of vascular bundles. It is also seen in these sections that the thickness of the cell-walls in one half of the pulvinus is three times as great as in the opposed half, and that all these cells communicate with each other by extremely fine canals. If the thick-walled portion of a pulvinus is disturbed with a bristle, no alteration is produced; but as soon as that side characterized by its delicate cell-walls is touched ever so lightly, it changes colour. It now appears a darker green, due to the fact that watery sap has been pressed out from the cells into the intercellular spaces. The slightest pressure is felt, accordingly, as a stimulus by the protoplasm in those

cells, and causes them to discharge a portion of their water into the adjacent spaces. By this means the turgescence in this part of the cushion is very much diminished, the tissue becomes flaccid, and in proportion as this flaccidity obtains the turgidity in the tissues of the opposite half of the leaf-cushion increases. It seems that a portion of the water given up by the stimulated protoplasm is forced into the opposite tissue, and that thus the turgidity there is augmented. Such a contrast in the turgidity of the two halves of the pulvinus cannot be without influence on the strand of vascular bundles lying in its centre; it becomes bent in the direction of the diminished turgidity, and the leaflet, whose midrib is formed by a continuation of the said vascular bundle-strand, follows this movement.

In nature, of course, stimulation of the protoplasm by contact of a solid body only occurs exceptionally. There the process described above is brought about by currents of air, and principally by falling rain-drops. Few phenomena have such a peculiar appearance as the movements which occur in the foliage of the already mentioned *Oxalis sensitiva* when rain comes on. Not only do the leaflets on which the first rain-drops fall, fold together in a downward direction, but all the neighbouring ones perform the same movement, although they have not themselves been shaken by the impact of the falling drops, and one is involuntarily reminded of the children's game in which sloped cards are placed behind one another lengthwise in a long series, and the fall of the outermost card, produced by the touch of a finger, causes in a moment the collapse of all the others. But it is not enough that the opposite leaflets, until now flatly outspread, are depressed by the shaking. The movement is continued to the common leaf-stalk bearing the numerous pinnæ. This also bends towards the ground, and hangs down apparently prostrated, in consequence of the alteration of turgidity in the pulvinus at its base. The rain-drops now slide over the bent leaf-stalk, whose point is turned towards the ground, and down over the depressed leaflets, and not a drop remains behind on their delicate surfaces.

The transmission of the stimulus, at first received only by a single leaflet, to the neighbouring leaflets and common leaf-stalk, and finally even to the whole plant, reminds one strongly of the like process in the leaves of the Sundew and of the Venus's Fly-trap. It also recalls the transmission of the stimulus in the protoplasm of lower animals, and is indeed to be explained in a similar manner. Probably the protoplasmic masses of the sensitive groups of cells in all pulvini are connected together by continuous delicate protoplasmic threads penetrating the cell-walls, and the molecular disturbance of the protoplasm, produced by the stimulus, although at first it comprehends only a single cell, is transmitted like an electric current in telegraph wires over the masses of protoplasm, strung together in close connection, and linked by the delicate plasma-threads; thus the same phenomenon is produced in all, viz. contraction of the cells and a forcing out of cell-sap into the intercellular spaces.

The other sensitive plants behave like the above-described *Oxalis sensitiva*, except that there is a difference in the direction in which the leaves fold together.

Æschynomene Indica, an elegant herb-like plant with papilionaceous flowers and extremely delicate doubly-pinnate leaves, as well as the Indian *Smithia sensitiva* (which likewise belongs to the Papilionaceæ), fold their leaflets together above, and

Fig. 134.—*Mimosa pudica* in day and night positions.

depress the common leaf-stalk directly the first rain-drop has produced a shaking. The same applies to several mimosas (*Mimosa pudica, sensitiva, casta, dormiens, humilis, viva*), of which the first, a species native in Brazil, is represented in fig. 134. In these mimosas there is really to be noted a threefold movement; first of all the tiny leaflets fold together above, and at the same time direct themselves a

little forward, so that each in front is partly covered over by the one immediately behind it; then the four ribs or axes, beset with the tiny leaflets, move towards one another like fingers which had been outspread and are now closed together; and thirdly, the common leaf-stalk, bearing in front the four axes, droops downwards. The leaflets of several species of wood sorrel which have clover-like or fan-like leaves, and not pinnate leaves like the above-mentioned *Oxalis sensitiva*, also fold their leaflets together when shaken by rain-drops. In these species of wood sorrel, however, we have again a way of diverting water, essentially differing from that above described. The common leaf-stalks do not bend towards the ground, but remain erect; on the other hand, the drooping leaflets fold slightly along the midrib, each of them forming a shallow groove, and as the rain water trickles on to the delicate leaves, and then flows through these channels to the ground. (Cf. fig. 90 [8], the lowest leaf, whose three leaflets are beginning to droop and to fold.)

From the above it is indeed evident that one benefit which the sensitive plants obtain by the sudden folding together of their leaflets lies in the rapid diversion of the falling rain-drops thereby rendered possible. By this we do not imply that this is the only advantage which ensues from the movements described. It frequently happens that dry, gusty winds and drifting sand and extraordinary noon-tide heat cause the folding of the leaflets. In the last-mentioned instances it is rather the danger of excessive transpiration which causes the plants to place the broad surfaces of their leaflets vertically, and all observations go to show that the leaflets can escape very various dangers by the assumption of the so-called sleep position—in the clear night, the loss of heat by radiation towards the starry sky; in the hot mid-day, drying up in consequence of rapid evaporation; in rainy weather, the breaking up of the tender leaves and their inclination towards the ground, as well as the collapse of the whole plant under the weight of the falling drops in a sudden severe downpour of rain. It is possible that yet a fourth advantage is obtained by these movements. Grazing animals which sniff the delicate leaves of the sensitive plants and disturb them with their mouths are perhaps astonished and frightened at the sudden movements of the leaflets, and abstain from eating these uncanny plants, especially when between the descending leaflets pointed rigid spines become visible, as is especially the case in many mimosas.

It cannot be too often insisted that the same and similar contrivances, as well as the same and similar processes, may have a very different significance according as they occur in this or that plant, in this or that habitat, and under these or those climatic conditions; just as, on the other hand, several advantages can be simultaneously obtained by one and the same contrivance. Thus for instance, the position which the leaves emerging from the buds in spring assume is very instructive. When the vegetative activity is interrupted by a cold winter, and when, moreover, the temperature occasionally in clear spring nights sinks below zero, the surfaces of the leaves just escaping from the buds are regularly placed vertically (cf. fig. 90). During the day excessive transpiration from the still thin-

walled tissues is prevented by this position, and during the night the vertical position of the young leaves has this advantage, that by it radiation, that is to say, excessive loss of heat, is hindered. The young not yet completely developed foliage is in both these respects very sensitive, much more so than adult foliage, and this depends upon the fact that the latter is comparatively poor in watery contents, and the composition of the protoplasm has become altered. It may happen that in the same plant, under the same conditions of habitat and like conditions of temperature of air and soil, while the young leaves perish after bright nights in consequence of too great loss of heat, the fully-developed leaves suffer no injury. This brings us to the question, Wherein the damage to plants caused by great loss of heat actually consists?

FREEZING AND BURNING.

Pancratius, Servatius, and Bonifacius, whose names stand in the calendar against the 12th, 13th, and 14th of May, have popularly been called "Eismänner" in southern Germany and Austria. They have received this nickname on account of the fall of temperature which takes place every year about the middle of May, the cause of which is not yet fully explained. Later in the summer such falls in temperature, connected with cooling of the atmosphere on a large scale, occur on certain days with some regularity; but these have not received so much notice because they are not so dangerous to field products, fruit and wine, as the relapses about the middle of the month of May. Moreover, although really cold days occur in June or July, they are never followed by a frost, while the three "Eismänner" of May usually bring with them severe frosts at night, even in the mildest regions of Central Europe, thus doing incalculable mischief to vegetation.

What first of all strikes us in a frozen plant-organ is that it has completely lost its elasticity. On bending and pressing back with the finger the frozen, stiffened foliage-leaf, a permanent fold is immediately produced; the leaf is broken along this fold, and can no longer resume its former position. At the time of breaking a noise is heard like the crushing of pounded ice, and as a matter of fact it is actually crystallized ice formed in the interior of the leaf which is broken by the pressure and causes this crunching to be heard. As the temperature rises during the day, the frozen plants become thawed, but most of them retain no longer the elasticity which they possessed before the frost. The leaves hang down flaccidly, are of a different green, and are more transparent than formerly. The surface is damp, and the epidermis is easily detached from the deeper tissue-layers. Gradually the languid leaves shrivel up, become dried, and assume a brown or black colour. They entirely resemble burnt or charred leaves, and the farmer says that the frost has burnt them.

What takes place in the interior of the plant on account of this freezing? The idea which botanists once held is as follows: the watery cell-sap of the plants stiffens to ice; but the ice takes up a larger space than was occupied by

the fluid cell-sap, and consequently the walls of the cells are torn and burst like a glass bottle in which water has frozen. A tissue whose cells are rent can, however, no longer perform its functions. Moreover, although the ice melts by and by, the damage to the ruptured cell-walls is irreparable. Besides, the cell-sap streams from the cell-chambers of a thawing plant, and the leaves and stem which have thawed after freezing are seen to be not only blackened, soft, and pulpy, but are also covered over with a watery film which is never absorbed again into the interior.

Renewed investigation has shown that this idea of the freezing of plants needs revision. First, in that no rupturing and bursting of the cell-walls occurs by the pressure of the ice formed in the interior of the cells. In the tissues of plant-organs surrounded by air the formation of ice does not usually commence in the interior of the cells, but in the intercellular spaces; and the ice-crystals are first formed in the interior of the cells only in those aquatic plants in which intercellular spaces are absent.

If *Nitella syncarpa,* belonging to the Characeæ, which is met with in the clear water of lakes and pools in Central Europe, is exposed to a temperature of 0° C., its vital activity is not disturbed. Even the streaming of the protoplasm in the cells is still very active, and even if by further cooling of the surrounding water to $-2°$ needles of ice are formed, the streaming of the protoplasm may still be recognized. The cells are indeed somewhat compressed by the ice-needles, but the protoplasm is never killed, even at $-3°$. It first begins to shrivel up between $-3°$ and $-4°$, gives up a portion of its water, shrinks away from its cell-wall, forms a folded, contracted sac in the middle of the cell, whilst the water excreted stiffens into ice between this sac and the cell-wall. If this *Nitella* be again exposed to a higher temperature the ice melts, the protoplasm expands, and lies close to the cell-wall; but it is incapable of again producing the streaming movement; it has ceased to live; its molecular constitution has evidently become so fundamentally altered by the separation of water from it that a reconstruction is no longer possible.

In the stems and leaves of plants surrounded by air, the ice always first arises, as remarked above, in the intercellular spaces. But since usually air, and not water, is contained in the intercellular spaces, the water stiffening into ice in them must have been first excreted from the neighbouring cells shortly before the freezing. And this is what actually happens. The structure of the ice-crystals plainly shows that the water has come from within through the cell-wall to the exterior, and that not once, but over and over again; for on the outer walls of the cells which face towards the intercellular spaces the ice is seen in the form of small discs placed above one another and combined into pillars, and these discs can have been only gradually formed one after the other. This observation, however, raises the questions, What portions of the cell give up the water? and why does the water freeze in the intercellular spaces and not in those places which it occupied before the frost? In answer to these questions it must first

be remarked that the water absorbed by the plants only partly enters into chemical combination with the materials of the cell-body and cell-wall; that another part, which we have called the water of imbibition, is not chemically combined. The cell-wall and cell-body are saturated with this latter, and the cell-sap in the vacuoles of the protoplasm also contains a large quantity of such water. In the cell-sap it appears as the solvent of the acids, salts, and other materials there present. The water by which the protoplasm and cell-walls are saturated, and which we must imagine filling the interstices, like capillary spaces, between the groups of molecules, is indeed held fast by the molecules of the protoplasm and cell-wall, and the water in the cell-sap by the molecules of acids and salts, but yet certainly not so energetically as the chemically-combined water in the albuminous substances of the protoplasm.

What happens now in a body which holds fast the water in its smallest interstices, like paste, for example, or in which the water appears as a solvent as in an alum solution, when warmth is withdrawn, and when it is cooled down to the freezing point of water? It is very remarkable that the water does not immediately stiffen into ice as long as it is retained in the capillary spaces, or as a solvent, and many salt-solutions can be cooled down to 5° C., some even to 10°, below zero without freezing. When at length under the influence of still lower temperatures a stiffening occurs, a separation has always taken place previously; the water has run together from the finest interstices of the paste into its larger spaces; it is first changed into ice in these cavities, and the water of the salt solution has separated from the molecules of salt, and is then first changed into ice-crystals.

The same thing occurs, however, with the water saturating the cell-wall and protoplasm, and serving as solvent of certain materials contained in the cells. The formation of ice occurs in a very few species only on cooling the plant-tissues down to $-1°$; in most instances the temperature must sink to $-2°$ or $-3°$ in order that ice may be formed in the cooled tissue. And indeed the water here has separated from the molecules by which it was hitherto held fast before it congealed, and it does not freeze in the interior of the cells, but outside them in the intercellular spaces. In order that the water should get from the interior of the cell into the adjoining intercellular spaces, a pressing and squeezing is necessary, and this pressure can only proceed from the living protoplasm in the cell-chambers; consequently the process of freezing can be most correctly represented in this way, viz. that the protoplasm becomes stimulated and roused by the lowering of the temperature to transport a portion of the water from the interior to the exterior of the cell, by means of contraction and pressure. What happens there is accordingly not unlike the excretion of watery sap into the intercellular spaces in the stimulated pulvini on the leaf-stalk of *Mimosa*; but the advantage obtained by the excretion of water in the two cases is very different. In the cooled leaves the benefit of course is to be sought for in the fact that the living portion of the cells is protected from destruction as long as possible by the formation of ice-crystals in the inter-

cellular spaces. If the water were forthwith frozen inside the cells, between the groups of molecules of the living cell-body and its wall by a few degrees of cold, fundamental displacements and disorganizations of the groups of molecules would be unavoidable. On the other hand, the ice-crystals on the exterior of the cells do not produce such destruction. In the intercellular spaces they can form large clusters, the spaces may be even enlarged by them, and the adjoining portions of tissue may be compressed and split, without a disorganization of the molecular structure of the living cells occurring simultaneously.

It is shown by numerous other phenomena that the excretion of water described does not connote the death of the living cells. It is also beyond doubt that the excreted water can be again received back subsequently under favourable conditions; and that by slow thawing of the ice formed in the intercellular spaces, the water again returns to the places it previously occupied within the cell. If, on the other hand, the cells are no longer able to take back the separated water, or if the cold becomes so severe that finally the water retained by the protoplasm and indispensably necessary to its existence, becomes changed into ice, then a disorganization of the molecular structure is the natural consequence; or, in other words, the protoplasm of the cells in question has been killed by the loss of heat. Then we say the plants are frozen dead.

Thus the difference between mere freezing and freezing to death is made clear; and at the same time the experience of gardeners is confirmed, that the former is not necessarily attended by the latter.

At what degree of cold freezing occurs, and at what freezing to death, depends first of all on the specific constitution of the protoplasm of the various species, but also, in each individual species, upon the stage of development arrived at by the organs exposed to the cold. Just as the water in various salt solutions becomes changed into ice at various temperatures, so the protoplasm of one species exhibits a different behaviour to that of another. It has been mentioned above that the hydrophyte *Nitella syncarpa* is frozen at a temperature of −4° C. Other aquatic plants bear a much greater degree of cold without their protoplasm being killed. *Sphærella nivalis*, which produces the red colour of snow, is exposed in the winter for months to a temperature of −20° C. in Arctic regions, and is not destroyed thereby. This *Sphærella* is also frequently exposed to very severe cold on the snow-fields of the Alps during winter nights, and the same remark applies to various species of the genera *Epithemia* and *Navicula* and to other Diatomaceæ which are to be found together with *Sphærella nivalis* living on the glaciers. It may be mentioned here in passing that there are also animals which live with these unicellular plants in the ice regions, and are not killed although they remain frozen for months. As soon as they thaw, these Rotifers bring their cilia into action again; the black Poduras, known by the name of glacier-fleas, take their flying leaps, and the spotted spiders again stride with their long legs over the sun-illumined ice-fields; while, on the other hand, the insects driven by the wind to these glaciers are in a very short time killed by the frost

The same thing occurs in land-plants and lithophytes as with animals and aquatic plants. Plants which closely resemble each other externally and show great similarity in their anatomy may yet behave quite differently in the matter of freezing. While the Stone Pine and the Shore Pine (*Pinus Pinea* and *Halepensis*) cannot bear the frost of winter, the Arolla Pine and Bhotan Pine (*Pinus Cembra* and *excelsa*) flourish in regions where the trunks and acicular leaves of all the trees are cooled down for weeks to $-20°$. *Rhododendron Ponticum* freezes at $-2°$, but *Rhododendron Lapponicum* survives the severest cold of the northern winter. If Echeverias are brought out of the greenhouse on a cold autumn night into an open place where the temperature falls to $-1°$, they will be irretrievably lost; while most of the European succulent plants closely allied to the Echeverias, and agreeing with them in the structure of the fleshy leaves, endure the same degree of cold without injury—not only for a night but even for weeks. The northern *Sedum Rhodiola* and several Alpine species of house-leek growing on the narrow ledges of rock faces in the high Alps (*e.g.* *Sempervivum montanum* and *Wulfenii*) are exposed for weeks to a temperature of $-10°$, and yet the protoplasm of their fleshy leaves does not freeze. There are also a number of biennial and perennial plants which cannot actually be called succulents, but which nevertheless form smooth, turgid leaves in the autumn arranged in rosettes lying on the ground, outwardly in no way protected against loss of heat. The leaves of these rosettes are exposed to the greatest cold in regions where the winter is severe, especially when little or no snow has fallen, and the temperature of the succulent tissue is often cooled down to $-20°$, and yet the protoplasm is not killed. The Scurvy Grass (*Cochlearia officinalis*) is, in this matter, particularly worthy of notice. It would naturally be expected that its smooth, turgid, dark-green leaves would be killed with the first hoar-frost, while in reality they endure a very considerable cold without the slightest injury. There are few places on the earth where such a severe winter climate prevails as on the shores of Pitlekaj on the northern coast of Siberia, where the *Vega* expedition passed the winter of 1878–79. In November the mean temperature amounted to $-16{\cdot}58°$, in December to $-22{\cdot}80°$, in January to $-26{\cdot}06°$, in February to $-25{\cdot}09°$, in March to $-21{\cdot}65°$, in April to $-18{\cdot}93°$. But these were only the averages; on many days the temperature fell to $-30°$, and $-40°$, and once the minimum even reached $-46°$ C. On the summit of a fairly high sand-hill over which the icy north and north-east wind swept almost uninterruptedly, a plant of Scurvy Grass (*Cochlearia fenestralis*) was observed. This plant had begun to bloom in the summer of 1878, and had also partly developed fruit. When the winter began, however, this *Cochlearia* still possessed unripe fruits, flowers, and flower-buds as well as succulent green foliage-leaves; and it was to be expected that the delicate succulent tissue would be completely destroyed during the long winter under the influence of the continuous cold. But in the summer of 1879 the plant, whose tissue had undoubtedly been cooled down for a long time to $-30°$, and frozen, began again to grow, and continued its growth where it had been interrupted at the beginning of winter. The leaves resumed

their functions as in the previous summer, the flower-buds opened, and new inflorescences sprang from the axils of the leaves, proving that the protoplasm of this plant had not been killed even by a temperature of $-46°$.

Myrtle and orange trees freeze dead from $-2°$ to $-4°$, cypresses and fig-trees from $-7°$ to $-9°$; vines at -21, oaks and beeches at $-25°$, plums and cherries at $-31°$, and apple and pear trees at $-33°$, and this can only be explained by the specific constitution of the protoplasm. We are forced to assume that the cell-body is destroyed in one case by a certain temperature, and in another by a different temperature, in the manner already described.

It has been previously remarked that the temperature at which freezing takes place also depends upon the stage of development of the plants. It is generally known that woody trunks and branches, foliage, and flower-buds, and especially seeds bear quite extraordinary winter temperatures when they have been poor in water in the autumn. In Yakutsk and Werchojansk in Siberia, where the mean temperature in January amounts to $-42·8°$ and $-49·0°$, and where $-62·0°$ and $-63·2$ (the lowest temperature hitherto generally observed on the earth) were noticed, where for months the temperature in the shade does not rise above $-30°$, numerous herbs and shrubs are found whose upper organs are exposed for weeks to a degree of cold at which mercury freezes; even birches and larches flourish there with the most vigorous growth, and there can be no doubt that the wood and buds of these trees are every year cooled down for a long time to $-30°$, and yet are not frozen. Moreover, every winter the wood of the juniper and of spruce, of silver firs and arollas sinks down to $-10°$ in inclement situations on the Central European mountains, and the evergreen leaves of these woody plants become cooled far below the freezing point of water without suffering the slightest damage. On this account the seeds inclosed in the berries and cones of the trees named bear the lowest temperatures without injury, which is so much the more remarkable since these seeds require two summers for ripening, and therefore must pass through the severe winter of the first year in a still unripe condition. The seeds of other plants also are exposed to great cold through the winter. Thus, for example, those of the Laburnum (*Cytisus Laburnum*) do not fall off as soon as they are ripe, but remain hanging to the sides of the dehisced pods, and as these are not detached from the branches until the following spring, the temperature of the seeds during the winter falls far below zero. They nevertheless maintain their germinating powers. Laburnum seeds, which had been during the winter for weeks under the influence of a temperature of $-15°$, germinated in the following summer, and so had evidently suffered no injury from the cold. Other seeds, too, even from tropical regions, which had been experimentally subjected to temperatures of $-40°$, were not found to have lost their germinating capacity, and consequently their protoplasm had not been killed even by this excessive temperature.

Since, on the other hand, it is known that the *young* fruits and seeds of the laburnum, and still more those of tropical plants, are already congealed by lowering the temperature to $-2°$, it follows that portions of that same plant in various

stages of development are affected differently by the lowering of their temperature below the freezing point. For the majority of plants the rule holds that death in consequence of frost occurs the sooner, the younger and richer the tissues in question are in water. The foliage of beeches, hornbeams, and deciduous oaks, which is not killed in the autumn, even after repeated frosts, withers, shrivels, and dries up when young if the temperature sinks below zero only for a single night in spring. Even many Alpine plants which bear very low temperatures without injury, when completely developed, may suffer harm if they are surprised by a frost at the period of most active growth. When on one occasion at the end of June the temperature sank to $-6°$ on the mountains near Innsbruck, already free from snow, at an altitude of 2000 metres, the young foliage-leaves of the Rhododendron (*Rhododendron hirsutum*), which had just sprouted, and were not yet fully grown, were destroyed on all the plants. They became brown and dried up, while the old fully-formed green leaves, remaining on the same plants from the previous year, underwent no alteration from the frost.

Such phenomena can only be explained by the assumption that in young, undeveloped organs much water is present, and is not under the control of the living protoplasm. As such water we may consider that which is conducted from the roots to the green tissue, to be there liberated in the form of vapour; that which mounts through the vascular bundles of the stem, streams through the veins of the leaves, under certain circumstances is even forced into the intercellular spaces, and passes out by the water-pores in the form of drops. This water is not retained by molecular forces, nor protected against freezing, but turns into ice even at a temperature of $-1°$. Since it is abundantly present in the young tissue when freezing takes place, extensive ruptures and mechanical injuries to the water-conducting tubes and rows of cells are unavoidable. But if the conduction of the crude food-sap is interrupted in a young plant-organ during its growth, transpiration in it can no longer occur properly, and the transpiring cells become withered and dried up even although their protoplasm should have suffered no direct harm from the frost.

Naturally connected with this discussion is the question whether a plant can freeze at a degree of temperature above that of the freezing-point of water. By the majority of gardeners this question would be answered in the affirmative, and their reply would be founded upon the fact that tropical Acanthaceæ, variegated-leaved *Coleus*, basils, melons, tobacco-plants, &c., become withered, dry up and die if they are exposed for only a single night to a temperature of $+2°$. In spite of the great outward resemblance between this phenomenon and freezing, it must nevertheless not be called freezing, for the most distinctive processes of the freezing of living protoplasm, viz. the excretion of water from the cell-body, the hardening of this water into ice, and its inability to return to the cell-body, do not occur in plants which are destroyed under the influence of temperatures above zero. It has been clearly shown that this so-called freezing of plants at temperatures above zero is really a drying-up in consequence of the disproportion between the transpiration from the leaves and the absorption of water by the roots. In consequence of the

fall of temperature in the soil, the absorbent activity of the roots is so restricted that the loss of water by the leaves through evaporation can no longer be replaced. The leaves then become flaccid, shrivel and dry up, are blackened, and look exactly like leaf-structures which have been killed by frost. It can be demonstrated by a very simple experiment that the cause of death is only the fall of temperature in the soil. If on autumn nights, when the temperature falls to $+1°$ or $+2°$, "very sensitive" *Coleus* plants in pots are brought from the warm greenhouse into the open, the pots not being protected against cooling, these plants dry up even the next day. If, on the other hand, the plants are sunk in warm sawdust over which cotton-wool is strewn, and thus care is taken that the temperature of the earth in the pots does not sink below $+7°$, then the *Coleus* does not dry up, and generally suffers no harm even although the temperature of the air and of the air-surrounded leaves should fall during the night to $+0·5°$. Since the conduction of water to the transpiring leaves is sustained by the warmth of the soil, these leaves may be protected from the so-called "freezing" even when they cool down to $+0·5°$.

Do means also exist by which plants may be protected from actual freezing? To this question the answer follows naturally from the above discussion about the real nature of freezing. If the plants in question can be hindered from assuming that temperature in which their protoplasm is killed, then, of course, a protection against freezing may be afforded. Usually bad heat-conductors are used as protective agents. The plant organs to be protected are clothed with dry straw and twigs, or covered with dried foliage. In regions with continental climates vines are protected against freezing by surrounding the lower portions of the stock with earth. Often plants are also protected by heaping up snow, and gardeners very generally use snow as an excellent protection against freezing. As a matter of experience numbers of plants perish with us during those winters in which no snow falls, while they survive without injury the coldest periods of winter when the snow is abundant. Many species of shrubs and low trees, of which only the lower half is snowed up, while the upper half rises above the surface are found after severe winters to be frozen from the apices of the branches down to the level to which the snow has reached. This happened, for example, in the Vienna Botanic Gardens (1880) with several young trees of the deodar (*Cedrus Deodora*), with the bushes of *Fontanasia jasminoides*, and with shrubs of many species of jasmine and indigo. But all these protective agents, twigs, straw, leaves, earth, and snow, fulfil their function only in neighbourhoods where the cold period is of comparatively short duration. In reality they ward off only the first onset of cold, and their principal use lies in the fact that the radiation of heat from the covered portions is retarded. In long and continuous cold the temperature of the coverings not only gradually sinks, but finally that of the covered bodies also, and in Yakutsk a plant whose protoplasm is killed at $-10°$ can no longer be protected even by the thickest covering of straw, leaves, or earth.

Moreover, in nature we can only speak conditionally of a natural protection against freezing, and only in those regions where periods of great cold alternate

with milder intervals during the winter, and where as a rule a warmer day succeeds the cold night, which is the case wherever the sun does not remain during the winter below the horizon for weeks or perhaps months. All coverings which protect from freezing in temperate zones are therefore entirely useless in Arctic regions. The snow which, as stated, is in the north temperate zone one of the best protective measures against severe temperatures, cannot in the Arctic regions at all hinder the penetration of the cold. Kane found the temperature in North-west Greenland at 63 cm. under the snow to fall to $-21{\cdot}3°$ and to $-16{\cdot}3°$ at 126 cm. below. The observations which were undertaken during the wintering of the Swedish Polar Expedition in Mussel Bay on the north coast of Spitzbergen, showed that on the 14th February 1873, when the temperature of the air was $-35°$, the snow had fallen to $-26°$ at 26 cm. below the surface, and at a depth of 35 cm. to $-20°$. On the 23rd February the snow at a depth of 30 cm. showed a temperature of $-21°$, while the temperature of the air was $-32°$. On the North Siberian coast the snow at a depth of 30 cm. was found by the *Vega* Expedition on the 22d March to be cooled down to $16{\cdot}1°$, and the earth below it to $-15{\cdot}1°$, while the temperature of the air was $-18{\cdot}2°$. At the middle of March the sandy soil penetrated by the roots of the Northern Bent Grass (*Elymus mollis*) exhibited at a depth of 63 cm. a temperature of $-20°$.

It is quite different in the north temperate zone. When the sun shines on the snow, if only for a few hours of the day, it becomes warmed and usually melted at the surface. In the Alps, during the shortest days in December, when the temperature of the air in the shade is $-10°$ to $-15°$, melted drops may be seen in mid-day trickling down from the sun-illumined roofs of the hay chalets situated high up on the mountain slopes. Three Swiss, who had determined for the purpose of meteorological observations to pass the winter of 1865–66 in the hut situated at an altitude of 3333 metres on the Matterhorn, observed on the 18th December, 1865, and on several other days, that in the sunshine the snow was melted. When the sun sets behind the mountains the melted water, of course, again freezes, but the next day the same process is repeated, while in Arctic regions, in the months of uninterrupted winter night, the fallen snow remains powdery. On mountains of the temperate zones, in consequence of melting under the influence of the sun's rays and the succeeding hardening during the nights, the superficial layer of snow forms a crust of ice which in time becomes so thick that wide stretches of snow-field may be traversed without breaking through it.

This alternation of thawing and freezing in the upper layers of the winter coat of snow has this important use, that in neighbourhoods where the sun shines in the winter the deeper layers of snow, and the solid earth bearing the snow, are never so much cooled as in the far north, where the cooling may continue for months, and where, as the above figures show, it actually does so continue. Minimum thermometers which were placed in the earth in the year 1869 on various mountain heights in the Tyrol, and at the end of the winter were dug up, showed the following temperatures: On the rocky summit of the Hafelekar, at Innsbruck.

at an altitude of 2343 metres, and 40 cm. below the surface, $-5·3°$; on the north side of the summit of the Blaser, at Trins, at an altitude of 2239 metres, 40 cm. below the surface, $-4·0°$; on the northern slopes of the Patscherkofel, at Innsbruck, 1535 metres above the sea-level, 60 cm. below the surface, $-2·9°$. The layer of snow lying on the ground at these three points was not a thick one, and varied from 30 to 60 cm. Where the snow-layer was at least three times as thick, the minimum thermometer gave the following results: On the south side of the summit of the Blaser, at Trins, at an altitude of 2239 metres, 40 cm. below the surface, $+0·1°$; rather lower on the same mountain, viz. at an altitude of 2086 metres, near the cottage of my experimental garden, under a snow-drift 3 metres thick, $+0·2°$; on the Patscherkofel, at Innsbruck, 1921 metres in height, in the vicinity of Kreuzbrunnen, 65 cm. below the surface of the ground, $+0·1°$; near the Heiligwasser, at Innsbruck, at an altitude of 1261 metres, where the winter coat of snow had attained a thickness of almost 2 metres, 75 cm. below the surface, $+1·35°$. These statements sufficiently show what a great significance is to be assigned to snow as a protective measure against cold in those regions which are not deprived of the sun in winter-time. While the temperature of the soil penetrated by roots of plants sank even under deep snow to $-20°$ on the winter station of the *Vega* in Siberia, the soil occupied by the roots of plants on the Alpine heights of the Tyrol in places covered with abundant snow, was never once frozen, and where the snow layer was very thin, was cooled down only to $-5·3°$. Accordingly in the Alps, and generally in high mountains of the north temperate zone, a thick layer of snow plays the part of an excellent protective measure to the soil, and consequently to the plants rooted therein.

There are also plants in Alpine regions which are apparently dependent upon this protective measure, and whose structure makes it possible for them to survive through the severe winter hidden under thick masses of snow. To these belong, in the first place, numerous bush-like woody plants of which *Pinus humilis* represented opposite may serve as an example. The stems of these pines are not erect like those of other species, but assume a horizontal position even when they attain a considerable thickness. Stems of even 20 cm. diameter, which would certainly be able to sustain the ample crown in an erect position, grow almost parallel to the ground without, however, directly resting upon it. In this respect it is very remarkable that on the slope of the mountain the growing end of the stem is always directed towards the valley, and it is also noticeable that this peculiar habit of growth occurs not only in the mountain pines growing wild in the Alps, but also in those raised from seed in the botanic gardens of towns, and must therefore be regarded as an inherent peculiarity. The boughs and twigs which curve upwards from the main stems are exceedingly elastic, and when pressed down stretch themselves out along the ground. Since all the boughs of the crown are turned upwards, we get here a considerable accumulation, so that in many old clumps of mountain pines the numerous boughs are so thickly crowded and so closely interwoven that progress through them is almost impossible. The extensive tracts

Fig. 135.—Mountain Pines (*Pinus humilis*) in the Tyrol.

of mountain pines are therefore avoided and left alone, and many of them have never been penetrated by the foot of man during their whole existence. Woe to him who has the misfortune to lose his way in such a tangled wood! The difficulties one has to encounter in a tropical primeval forest beset with lianes are not greater than those with which one must struggle in attempting to press forward here. Frequently the mountain pines grow so high that one is considerably overtopped even when standing upright by the highest prickly branches. It is perhaps possible to make a little progress by climbing over the horizontal, arm-thick stems, but it is vain to endeavour to find one's way and to gain an outlook. If we mount on one of the curved ascending boughs in order to see above the highest branches, the bough bends down to the earth under our weight, along with the stem from which it arises, and we again sink despairingly into the sea of the dark-green crowns. Just such a down-bending occurs, however, under the burden of the winter snow. If then by chance the ordinary mantle of snow is added to by that from avalanches, the pressure increases so much that the branches are pressed down to the soil. This process may go on to such an extent that even many branches, which in the summer stand a metre above the ground, lie in the winter directly on the soil on account of the snow pressure. When the snow melts in the following spring, and the branches are gradually lightened, they rise up again in consequence of their extraordinary elasticity, and resume that position which they occupied in the preceding summer. The process which is here carried on automatically strongly reminds us of the manipulations of gardeners, who in the autumn bend down rose-trees to the earth and cover them with non-conductors, keep them in this position throughout the winter, and not till the next spring raise them again and fasten them to erect sticks. In the summer the old leaves on the ends of mountain pine branches, which wave above the ground more than a metre high, may be frequently seen plastered over with earth and small stones, and anyone knowing nothing of the processes above described would not easily understand how these small stones had come to be fixed in these situations. As a matter of fact the earth which lies on the branches through the winter, moistened by the snow-water, forms the adhesive agent, which is so efficient that stones more than 1 cm. in diameter are attached by it to the old tufts of leaves. Many other Alpine shrubs behave like the mountain pines, as, for example, the Dwarf Juniper (*Juniperus nana*) and the Alpine Alder (*Alnus viridis*). In like manner the rhododendron bushes are also pressed to the ground by the snow, although not to such a great extent, and are thus protected against the great cold, and particularly against extreme radiation.

In forest regions the dry foliage, which falls from the trees and overspreads the ground and undergrowth to a greater or less thickness, appears also to be usually an excellent protective agent. This foliage layer is thickest in the beech forests of Central Europe, and the sheltered plants include the Woodruff, Lungwort, Hepatica, Asarabacca, Sanicle, and Waldsteinia (*Asperula odorata, Pulmonaria officinalis, Hepatica triloba, Asarum Europæum, Sanicula Europœa,* and *Wald-*

steinia geoides) maintain themselves beneath it, unfrozen, even in very severe winters.

Other plants, again, appear to be protected against extreme cold by the fact that they retire underground during the winter. Large numbers of bulbous and tuberous plants manufacture organic compounds in their green leaves in the warm sunbeams of summer, at once transmitting them below to their subterranean portions. There, thick stems and tubers, fleshy scale-like leaves, and the rudiments of new foliage and flowers (which, however, do not appear above-ground

Fig. 136.—Detachment of special shoots of *Potamogeton crispus*, for hibernation under water.

the same year) are produced from the materials supplied. Throughout the winter these structures remain buried in the earth, and are there protected against excessive cold, just like roots. After the winter is over, the flower-stalks and foliage-leaves, commenced in the previous year, rise up in order to bloom and fructify, and to form anew, in the sunlight, organic materials for the subterranean bulbs, tubers, and root-stocks. It is very interesting to notice that bulbs and tubers bury themselves deeper in the earth the more exposed their habitat to radiation and cooling, the more they are threatened with the danger that the earth will be covered by only a thin mantle of snow. While, for example, the bulbs and tubers of *Gagea lutea* and *Corydalis cava*, when growing in the black humus of beech forests under withered foliage, lie only a few centimetres below the surface, in open

meadows they are only to be found at a depth three or four times as great. The position of the tuberous roots of many orchids, and of the corms of the Meadow Saffron (*Colchicum autumnale*) may be actually used as marks to indicate how deeply in a given neighbourhood the ground is frozen, for these occur imbedded just at that depth to which the winter frost fails to penetrate.

The same thing is also observed in aquatic plants. In the still waters of lakes and ponds the plants bodily withdraw before the advancing cold of winter, and an actual retreat into the depths takes place. The Water Soldier (*Stratiotes aloides*) sinks down before the commencement of winter to the bottom of the lake, where it scarcely ever freezes; it passes the winter there, and does not rise again to the surface till the following spring. *Potamogeton crispus*, figured above, produces late in the autumn, near the surface of the water, shoots possessing short leaves which are detached from the old stem before the uppermost layer of water is frozen. These sink into the depths, and bore their way into the mud by their pointed lower extremities. There, in their winter quarters, where there is never any formation of ice, these sprouts are excellently protected against injury from excessive cold.

Erect trees and shrubs, which rise up column-like above the earth, are little affected by the presence or absence of a covering of snow upon the ground. Generally the leaves have been already shed, after they have delivered up such substances as they contained of value. The leafless branches and the next year's buds indeed remain above the ground, being thus exposed to the winter cold, which they must be capable of bearing without injury. The branches are covered with a tough and compact investment; and it would seem as if such a covering would be able to protect the portion clothed by it against cold better than a mere epidermis. For a very short period of cold weather such may be the case, but for a longer period even the thickest coat would be unable to keep the cold from the covered portions, just as little in fact as the bark on old boughs and trunks. In long-continued winters, with uninterrupted severe cold weather, the interior of the branches and trunks assumes the temperature of the environment, and it depends entirely upon the resisting capacity of the protoplasm whether the cooling is fatal or not. From various appearances it may be concluded that this resisting capacity is greater the better the opportunity afforded to the protoplasm of suitably preparing itself in the foregoing summer and autumn. If the summer was warm, and the autumn mild, if the advent of the first frost was much retarded, and the plant had time to become a chrysalis slowly, in preparation for the winter, then the branches do not freeze dead; but if the summer was cold and wet, and frosts appeared early in autumn, if the water of imbibition was not removed at the right time, and the wood, as gardeners say, is not "ripened", then a tolerably severe winter may result in the death of the branch, of the same branch, indeed, which perhaps in previous years survived without injury much greater cold.

Accordingly we always come back to this, that the freezing of a plant to death, or not, depends upon whether or not the condition of the protoplasm is such that its molecular constitution becomes permanently disorganized in consequence of the

cooling, and that the most effective protection must be sought for in the constitution of the protoplasm itself. Since we do not know the constitution of the protoplasm, it is idle to puzzle ourselves in surmises about it; this only being certain, that the resisting capacity of protoplasm differs much from plant to plant, as well as at different times in one and the same plant.

The results which have been obtained by the study of the *burning* of plants are analogous to those afforded by researches into the nature of freezing.

When a plant organ loses its capacity of absorbing food, of breathing, and of further development, in consequence of the rise of temperature, we say then that it is burnt. The outwardly visible appearances of burnt plants resemble exactly those which have been observed in plants killed by freezing; the green tissue is discoloured, exhibits a darker tint, is more transparent, fades and dries up, and neither the supply of water nor the reduction of the temperature can reproduce the previous conditions. The protoplasm in the interior of the cells is massed into balls, and is detached from the cell-wall; water is excreted, which had stood hitherto in molecular combination with the protoplasm. These observations can be followed very easily in aquatic plants whose cell-walls are so transparent that they allow us to see into the interior of the cell-chambers. If the cells of the water-plant *Elodea*, illustrated in fig. 5 [3] (page 25), are examined under the microscope while the temperature of the surrounding water is 30° C., the protoplasm will be seen to exhibit that active streaming movement described on p. 33. If the temperature is raised to 40°, the streaming becomes slower, and at 41° ceases entirely, although the protoplasm shows no other particular alteration. Even if the temperature is raised to 45°, and gradually to 50°, nothing is altered in appearance; not until 52° does any very noticeable alteration occur. Then the starch-granules imbedded in the protoplasm split up; the protoplasm shrinks together and forms clump-like masses around the fractured starch-granules. The protoplasm now becomes rigid, the albuminous materials in it are curdled or coagulated. Subsequently, if the temperature again sinks to 30°, it does not become again living and active, and we must therefore assume that its molecular constitution has suffered at 52° an irreparable alteration, in fact, that it has been killed.

In the main, therefore, burning depends upon the coagulation of the albuminous compounds, upon the destruction of the starch-granules, and the decomposition of the protoplasm. If the coagulation of the albuminous compounds and the alteration of the starch-granules were always brought about by one and the same temperature then probably all plants would be "burnt" at this same temperature. But such is not the case. The various albumens not only coagulate at different temperatures (viz. 60°–80°), but the point of coagulation of the same albumen is materially affected by the watery contents, and by the presence of salts and acids. When, for example, many salts are present, coagulation may occur at 50°. Nor does the destruction of the starch-granules always occur at the same temperature; large starch-grains, swollen with water, at 55°, smaller ones not till 65°;

and, in order that dry starch-grains may be destroyed, a still higher temperature is necessary. Under such conditions it is not to be wondered at that plants, whose protoplasm exhibits different coagulation points, should be "burnt" at very different temperatures. The processes which have been observed in the above-mentioned *Elodca* at 30°, 41°, and 52°, are seen to occur in other water-plants at other temperatures. In the cells of *Vallisneria spiralis*, represented in fig. 5 [2], the streaming of the protoplasm does not stop till 43° has been reached, and the protoplasm is not formed into balls in consequence of the coagulation of the albumen till 53°–54°. In the lattice-leaved *Aponogeton fenestralis*, growing in Madagascar, the coagulation and death of the protoplasm first occur at 55°. Many algæ bear even still higher temperatures. In the channels through which the hot water of the Carlsbad spring flows, dusky oscillarias flourish even at a temperature of 55° to 56°; in the springs of Abano, which reach a temperature of nearly 60°, *Sphærotilus thermalis* is to be found, and in the Solfatara at Naples, the side-walls of the rocky clefts, from which vapour issues at a temperature of 55° to 60°, are covered with a green film of algæ.

In plants which are not submerged in water, the watery contents as well as the specific constitution of the protoplasm have a material influence on the burning. If the exposed tissues are poor in water they can sustain much higher temperatures than when very turgid. The highest temperature which the turgid cells of lithophytes and land plants can endure without being burnt is in most cases 55°. In the sun, succulent plants can endure for a long time without injury temperatures of 50° to 53°. The spores of moulds (*Rhizopus nigricans* and *Penicillium glaucum*) have been seen to germinate and develop at from 54° to 55°. When dry, those cells and tissues which can be dried up without harm do not perish even under the influence of far higher temperatures. The crustaceous lichens adhering to the limestone rocks of the wild regions of the Karst of Istria and Dalmatia (*Aspicilia calcarea*, *Verrucaria purpurasccns*, and *V. calciseda*) are regularly exposed on cloudless summer days to a temperature of 58° to 60° without injury, and the edible lichen (*Lecanora esculenta*), illustrated opposite, is often heated in the deserts, along with the stone on which it grows, to fully 70°, and yet is not destroyed. Moreover, seeds which are deposited on the desert sands, and survive in this position the long periods of drought, do certainly assume the temperature of their environment, and although at noon this often amounts to 60°–70°, it does not injure these seeds; since, when the rainy season returns, they are roused from their summer sleep, and germinate in the cool and moistened soil. The highest temperature in the superficial layer of soil has been observed near the equator at Chinchoxo on the Loango coast. Here, in many cases it exceeds 75°, often attains 80°, and once attained to even 84·6°. Nor is this soil destitute of annuals during the rainy season, and without doubt the dry seeds of these plants have been lying for months in the sand, sometimes heated to over 80°, without losing their germinating power. It has been proved experimentally that seeds, which have been deprived by calcium chloride of as much water as

possible, are not killed even at the boiling point of water. Of various seeds from which water has been withdrawn for fifty hours, and which have then been heated for three hours up to 100°, those of duckweeds (49 per cent of the seeds experimented upon) still germinated; of vetches, 50 per cent; of garlic, 60 per cent; of wheat, 75 per cent; of sweet marjoram, 78 per cent, and of melons 96 per cent. Even of seeds previously dried, which had been exposed for about fifteen months to a temperature of 110° to 125°, a small percentage always germinated, and it is possible that there are species whose seeds bear without injury still higher temperatures.

From these experiments it is clearly shown that the albuminous substances in the protoplasm may give up with impunity much water, and that by this

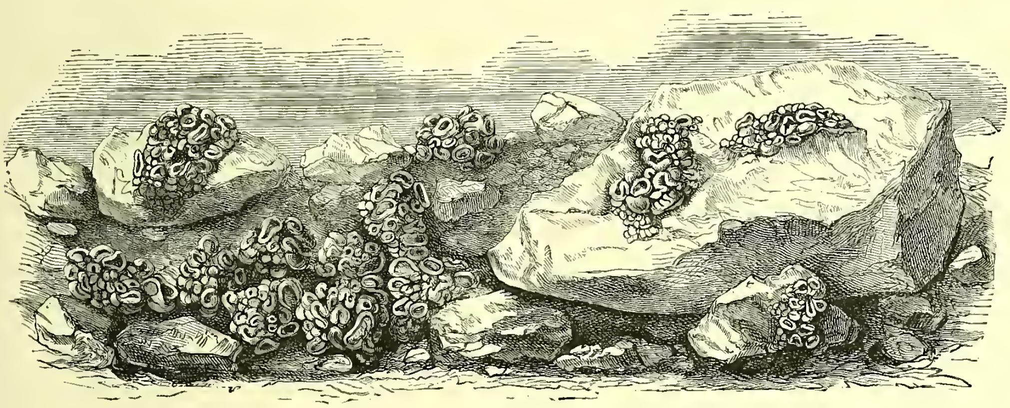

Fig. 137.—Edible Lichen (*Lecanora esculenta*) in the desert.

surrender a protection is obtained against coagulation and burning, up to a certain point.

In nature, most contrivances by which plants are protected against burning amount in reality to a periodic surrender of water. Lithophytes, especially crustaceous lichens, which are most threatened with the danger of being burnt, are so organized that they can give up a great deal of water in a very short time. They then become stiff and brittle, and can be rubbed into powder, and it appears scarcely credible that these dried-up structures can ever live again. In the rock-lichens the same thing occurs. Also several Volvocineæ, *Sphærella pluvialis*, and various other simply organized plants, living in shallow pools and ditches, dry up to dust along with the mud, after the evaporation of the water which had accumulated in their habitat, and are protected in this dried condition against burning. If the dust, which is warmed daily for several hours up to 60° during the period of drought, becomes moistened later on, all the tiny plants wake up again from their trance, and, as should not be overlooked, the rotifers and various infusoria, which are present in the same heated dust, again bestir themselves, flourish their cilia, and give evidence that the surrender of water at the right moment affords the best protective measure against "burning" for animal proto-

plasm also. In deserts and steppes, and in all regions where the earth is warmed up to 70° in hot rainless seasons, there are, it is well known, a great many annuals. When the hot period commences, leaves, stems, and roots are already dead, and the plants have scattered their seeds. These seeds, however, possess very little water, and yet can give up a portion of that they contain without injury; they are thus protected in the best way possible against being burnt.

One portion of the perennial plants of these regions throws off its foliage at the close of the rainy period, and lives through the hot, dry period with leafless and apparently dried-up branches; others expose the whole of their organs above the ground to burning, maintaining themselves below the soil only, where the earth never acquires such a high temperature; these sleep through the hot period as resting tubers, bulbs, and root-stocks. It should also be remembered here that in regions where high temperatures are not combined with great dryness, the excessive heat can be diminished by the evaporation from the succulent tissue, since, as is well known, evaporating bodies always undergo a cooling. Finally, the fact is to be considered that many plants choose places for their settlement where they are not exposed to burning, even on the hottest days of the year. Under the protection of shade-giving rocks, and wherever the sun's rays are not able to operate directly and untempered, the soil, even at the equator, may not exceed those temperatures at which succulent plant-organs cannot be burnt, and still less could the normal warmth of the air in shady places bring about such an effect; for the highest temperatures hitherto observed in the shade rise scarcely above 40° (42° in Abu-Arisch, in Arabia; 43·1° on the river Macquarie, in Australia), and at these temperatures the albuminous substances are never coagulated in any single plant.

The question now is how the results obtained from researches into the phenomena of freezing and burning can be brought into harmony with the earlier ascertained relations of heat to living plants, and especially with the theory of growth. We have conceived growth as a form of molecular work of living protoplasm, and we imagine the molecules and groups of molecules to be in a condition of heat-vibration of definite extent; or, in other words, that for all work, and especially for growth, a definite degree of heat is necessary. If the heat-vibrations exceed the fixed limit, the position and the mutual relations of the molecules in the protoplasm are completely altered, and disarrangements result which cannot subsequently be made good. The protoplasm has then lost the capacity of further maintaining itself and increasing—it is burnt and killed. The same happens if the intensity of the heat-vibration sinks below a certain degree. Then again changes are produced in the substance of the protoplasm which are irreparable, and are followed by death. Consequently, a superfluity as well as a want of heat can retard the molecular action of the living protoplasm which appears as growth, and can even completely stop it. And the interruption is brought about in the protoplasm of different species under the influence of different degrees of heat; just as water, alcohol, and mercury solidify at certain temperatures, and become vaporized at

certain others, so there is a temperature for the protoplasm of every species at which it freezes, and another at which it is burnt. But this leads to the conclusion that the molecules and groups of molecules in all protoplasm vibrate definitely as to extent and intensity so long as the protoplasm is living, even if it is not exactly performing that work which appears to us as growth—in other words, that a definite amount of heat is necessary to the maintenance of life even in protoplasm apparently resting; and that consequently it is not correct to suppose that all the heat supplied to the plants is used up in growth.

ESTIMATION OF THE HEAT NECESSARY TO GROWTH.

According to the mechanical theory of heat, which gives the best explanations of numerous phenomena of life, all motion can be converted into heat, and measured as such. Should it not be possible to apply this principle to the vegetable kingdom, especially to the phenomena of growth? Ought we not to be able to estimate definitely how much heat is required for plants for each of their performances within a definite period, and therefore to determine their heat-requirement as a constant numerical quantity? This question has often been put, and experiments have not been wanting to supply the answer. It would not be only of theoretical but also of great practical value, to be able to tell how much heat our forest trees, our cereals and other economic plants, need for the accomplishment of their yearly cycle of life, to know how much heat is necessary for the germination of this or that cultivated plant, how much in order that the germinated plants may blossom, and what degree of heat they require to produce ripe seeds of full weight and capable of germination. If it were practicable to determine those quantities of heat, which might be called the *thermal constants of vegetation*, we should be able to estimate beforehand from the heat-conditions prevailing in any particular place, whether this or that plant species would thrive, whether it could produce ripe fruits, and whether or not its cultivation would be advantageous and worthy of encouragement.

Hitherto the results obtained in this direction leave very much to be desired, but are nevertheless so interesting that they cannot be passed over in silence here. First of all, it has been proved with regard to the earliest phases of growth, the germination of spores and seeds, that not a few species are able to germinate even at very low temperatures. The seeds of the White Mustard, of hemp, of wheat and rye, of the Norway Maple, and of the wild violet, germinate at a temperature very near freezing, between 0° and 1° C.; others, such as the garden cress, flax, spinach, onions, poppy, beet-root, and the English rye-grass, germinate at temperatures between 1° and 5°; French beans, sainfoin, millet, maize, sunflowers, at temperatures between 5° and 11°; tomato, tobacco, and gourds at temperatures between 11° and 16°; cucumbers, melons, and cocoa beans not until above 16°. That is to say, that melon seeds, if placed in damp soil whose temperature lies below 15°, absorb, it is true, the moisture, and swell up,

but that those alterations which really constitute growth are not produced in the cells of the embryo at this temperature. Not until the temperature of the soil rises above 15° does the embryo elongate, and the radicle bore its way through the seed-coats. But all these figures would give by themselves a very incomplete idea of the heat-requirements of germinating seeds, were it not also ascertained how long the seed must be exposed to the given temperatures in order that its embryo should increase and develop. If a hen's egg is exposed for only two or three days to a temperature of 35° to 40°, it will not be hatched; hatching can only take place if the egg remains for 20–21 days under the influence of this constant temperature. With seeds the case is the same. The following is a selection of the results obtained in this relation:—

The seeds of	germinated at a constant temperature of	in No. of days.	The seeds of	germinated at a constant temperature of	in No. of days.
Gold of Pleasure	4·6°C	4	Pimpernel	10·5°	10
Pea	4·6°C	5	Maize	10·5°	11
Spinach	4·6°C	9	Millet	10·5°	13
Poppy	4·6°C	10	Coriander	10·5°	16
Beetroot	4·6°C	22	Sunflower	10·5°	25
Guinea grass	4·6°C	24	Tomato	15·6°	6
French Beans	10·5°C	3	Tobacco	15·6°	9
Timothy-grass	10·5°C	6	Cucumber	18·5°	5
Sainfoin	10·5°C	7	Melons	18·5°	17

If the number of days is multiplied by the temperature, the product may be looked upon as an empirical formula for the heat necessary to the process of germination. It may be considered that this product is of regular amount, and it is regarded as a "thermal constant". Thus, for purposes of comparison, the thermal constants for the germination of the seeds of the Gold of Pleasure might be expressed as 18·4, of the Poppy 46·0, of Maize 115·5, and so forth.

In these calculations, of course, only the constant temperatures of the soil not directly illumined by the sun's rays come under consideration. The matter becomes far more complicated when it is a question of determining the constants for other stages in the development of plants, such as the bursting of foliage from the buds, the opening of the first flowers, and the ripening of the first fruits. These phenomena of growth in the majority of plants in the open do not occur in the shade, but in the sun. Moreover, in the places under observation, the temperature is not constant, but changes from hour to hour, attaining its minimum shortly before sunrise, and its maximum in the first hours of the afternoon. Since experience has shown that the extent of growth is regulated according to the highest temperature in the sunshine, it follows that neither the shade temperature nor the mean temperature, but the readings of the maximum thermometer, exposed to the sun, must be used for the estimation of the constants in the above-mentioned phenomena of growth.

To obtain the thermal constants for foliage-production, flower-opening, and seed-ripening, of a plant growing in a situation illuminated by the sun, one must

add together the daily maxima of sun-temperatures from the first of January until the event in question takes place.

A selection of constants obtained in this way from observations extending over many years in Central Germany (Giessen) may be suitably inserted here.

Constants for the Issue of the Foliage-leaves from the Buds.

Gooseberry (*Ribes Grossularia*) 478°.
Hazel (*Corylus Avellana*) 1061°.
Beech (*Fagus silvatica*) 1439°.
Plane (*Platanus acerifolia*) 1503°.
Walnut (*Juglans regia*) 1584°.

Constants for the Opening of the First Flowers.

Hazel (*Corylus Avellana*) 226°.
Mezereon (*Daphne Mezereum*) 303°.
Snowdrop (*Galanthus nivalis*) 311°.
Sweet Violet (*Viola odorata*) 576°.
Cornel (*Cornus mas*) 576°.
Apricot (*Prunus Armeniaca*) 843°.
Corydalis (*Corydalis cava*) 863°.
Violet Willow (*Salix Daphnoides*) 968°.
Cowslip (*Primula veris*) 968°.
Norway Maple (*Acer platanoides*) 1100°.
Peach (*Persica vulgaris*) 1100°.
Gooseberry (*Ribes Grossularia*) 1138°.
Almond (*Amygdalus communis*) 1196°.
Gean (*Prunus avium*) 1265°.
Sloe (*Prunus spinosa*) 1265°.
Pear (*Pirus communis*) 1304°.
Bird Cherry (*Prunus Padus*) 1325°.
Apple (*Pirus Malus*) 1423°.
Plum (*Prunus domestica*) 1423°.
Alpine Woodbine (*Lonicera alpigena*) 1458°.
Oak (*Quercus pedunculata*) 1556°.
Lilac (*Syringa vulgaris*) 1556°.
Walnut (*Juglans regia*) 1584°.
Barberry (*Berberis vulgaris*) 1615°.
Poet's Narcissus (*Narcissus poeticus*) 1615°.
Hawthorn (*Cratægus Oxyacantha*) 1649°.
Lily of the Valley (*Convallaria majalis*) 1649°.
Horse Chestnut (*Æsculus Hippocastanum*) 1708°.
Peony (*Pæonia officinalis*) 1818°.
Laburnum (*Cytisus Laburnum*) 1818°.
Mountain Ash (*Sorbus aucuparia*) 1844°.
Norway Spruce (*Abies excelsa*) 1904°.
Plane (*Platanus acerifolia*) 2115°.
Elder (*Sambucus nigra*) 2313°.
Deadly Nightshade (*Atropa Belladonna*) 2346°.
Acacia (*Robinia Pseudacacia*) 2404°.
Scotch Pine (*Pinus sylvestris*) 2404°.
White Water Lily (*Nymphæa alba*) 2506°.
Arnica montana 2538°.
Tulip Tree (*Liriodendron tulipifera*) 2538°.
Rosa centifolia 2538°.
Fox-glove (*Digitalis purpurea*) 2640°.
Carthusian Pink (*Dianthus Carthusianorum*) 2640°.
Vine (*Vitis vinifera*) 2878°.
Broad-leaved Lime (*Tilia grandifolia*) 3033°.
Small-leaved Lime (*Tilia parvifolia*) 3274°.
Oat (*Avena sativa*) 3444°.
White Lily (*Lilium candidum*) 3378°.
Chestnut (*Castanea sativa*) 3660°.
Immortelle (*Helichrysum arenarium*) 3918°.
Ling (*Calluna vulgaris*) 4164°.
Trumpet-tree (*Catalpa syringæfolia*) 4275°.
Blue Aster (*Aster Amellus*) 4874°.
Syrian Marsh-Mallow (*Hibiscus Syriacus*) 4986°.
Meadow Saffron (*Colchicum autumnale*) 5024°.
Ivy (*Hedera Helix*) 5910°.

Constants for the Ripening of Fruit.

Wild Strawberry (*Fragaria vesca*) 2671°.
Gean (*Prunus avium*) 2778°.
Mezereon (*Daphne Mezereum*) 2935°.
Red Currant (*Ribes rubrum*) 3069°.
Gooseberry (*Ribes Grossularia*) 3596°.
Alpine Woodbine (*Lonicera alpigena*) 4164°.
Mountain Ash (*Sorbus aucuparia*) 4339°.
Barley (*Hordeum vulgare*) 4403°.
Apricot (*Prunus Armeniaca*) 4435°.
Apple (*Pirus Malus*) 4730°.
Barberry (*Berberis vulgaris*) 4765°.
Carthusian Pink (*Dianthus Carthusianorum*) 4874°.
Elder (*Sambucus nigra*) 4913°.
Pear (*Pirus communis*) 5024°.
Cornel (*Cornus mas*) 5416°.
Plum (*Prunus domestica*) 5780°.
Vine (*Vitis vinifera*) 5780°.
Peach (*Persica vulgaris*) 6004°.
Horse Chestnut (*Æsculus Hippocastanum*) 6034°.
Oak (*Quercus pedunculata*) 6236°.

Constants for the Commencement of Leaf-fall.

Bird Cherry (*Prunus Padus*) 6179°.	Hazel (*Corylus Avellana*) 6884°.
Small-leaved Lime (*Tilia parvifolia*) 6644°.	Gooseberry (*Ribes Grossularia*) 6884°.
Elder (*Sambucus nigra*) 6644°.	Beech (*Fagus silvatica*) 6884°.
Alpine Woodbine (*Lonicera alpigena*) 6759°.	Vine (*Vitis vinifera*) 6913°.
Pear (*Pirus communis*) 6788°.	Oak (*Quercus pedunculata*) 6979°.
Walnut (*Juglans regia*) 6816°.	Apple (*Pirus Malus*) 6999°.
Trumpet-tree (*Catalpa syringæfolia*) 6816°.	Chestnut (*Castanea sativa*) 7023°.
Violet Willow (*Salix daphnoides*) 6838°.	Gean (*Prunus avium*) 7023°.
Horse Chestnut (*Æsculus Hippocastanum*) 6863°.	Plane (*Platanus acerifolia*) 7145°.

Although the computations which have been made at different places and over several years, by way of trial, have given figures which do not differ materially from the above, and it seems as if these constants actually justified that term, yet confidence in them has been to some extent diminished by the following considerations.

With regard to the germination of seeds it is concluded from various phenomena that the heat liberated in respiration from the cells, as well as the temperature of the soil, has not a little influence also on the process of growth. Seeds in whose cells the protoplasm has once been set in action by an external impulse, perhaps by a minimum of radiated or conducted heat, respire with a fair amount of activity. In this way the reserve materials stored up in them are consumed, and so much heat is liberated that not only is the embryo able to develop, but heat may be even given up to the environment. Radicles of germinating maple and wheat seeds, which by chance were found in an ice cellar, were observed to grow down into the blocks of ice, and this could only have happened from the melting of the ice by the radicles, which push their way into the cavities formed, like the flower-buds of the Soldanellas already described. In many cases of observed germination it may therefore be doubted whether the growth of the embryo alone is to be laid to the account of the measured heat, supplied to the seeds from their surroundings. On the other hand, it is doubtful whether the heat (registered by the thermometer), which reaches the plants from outside, is employed only in growth. One part may be used in order to maintain the plant-organ in question alive; another portion may be useful in the production, and in the transformation and transmission of constructive materials, and only a residual portion can then participate in growth. But this is not all. It is also doubtful whether the positive heat entering the plants from outside, can be always completely disposed of, within the given space of time, in the various chemical transformations and molecular arrangements carried on in the interior of the plant, and whether an unused surplus is not sometimes present which should be really withdrawn from the calculation. It is tacitly implied in the reckonings that if the plants are exposed to a constant temperature of 20° for 12 hours, the total heat which was able to raise the mercury up to 20° in that time would also be turned to account by the plants. But that this is not so, is shown by the following observations:

No. of Hours required	for germination of the seeds of	at a temperature of	Constants so reckoned.
48 36	White Mustard (*Sinapis alba*), ...	4·6° 10·5°	220·8 378·0
72 48	Hemp (*Cannabis sativa*), ...	4·6° 10·5°	331·2 504·0
144 96	Flax (*Linum usitatissimum*), ...	4·6° 10·5°	662·4 1008·0
144 80	Maize (*Zea Mais*),...	16·1° 44·0°	2318·4 3520·0

From these observations it is easily gathered that in those instances in which the seed was exposed to a higher temperature, only a *portion* of the heat supplied was actually employed in germination, and that, therefore, the constants calculated on the basis of these observations are much too high.

If the thermometer could tell us the amount of heat actually needed within a certain time by plants growing together, then only might the constants reckoned from these readings be regarded as accurate and become useful for comparison. But these conditions are not fulfilled. Usually here the conclusions are only *post hoc propter hoc.* Thermometric readings are brought into calculation which include the surplus of heat not used by the plants, and consequently the constants are not the correct expression of the quantity of heat actually consumed in growth.

The bases on which the calculations are founded, for growing organs directly under the influence of the sun's rays, are much more uncertain than those for seeds germinating in shaded ground. Besides, doubts must arise from the fact that the sun's rays have a widely differing effect on foliage, flowers, and fruits from that which they have on the mercury of the thermometer. This defect may indeed be removed by using the same instrument in all observations and employing suitable corrections; but it is a more serious matter that we have no means of ascertaining how much light is changed into heat in growing organs exposed to the sun's rays. With increasing altitudes the intensity of the light increases, and its significance for growth increases in a corresponding manner. But it is impossible to determine these relations numerically, more especially to determine them in plants and thermometers observed in the open.

Nor must it be forgotten that the absorption of heat also depends upon the individuality of the plant observed, and upon the constitution of the protoplasm of the particular species. The seeds of the White Mustard are incited to growth even by temperatures little removed from the freezing-point, while the seeds of melons do not germinate until they have been exposed to the influence of a temperature of 18·5° C. for at least 17 days. This shows that every species has to a certain extent its own zero at which growth begins, and all calculations of the heat required for the growth of the stem and foliage of any particular species should always be reckoned only from this zero. Moreover, it is a matter of experience confirmed by all gardeners that higher temperatures are required for the development of flowers than for foliage, and that for the proper ripening of seeds higher temperatures still

are necessary. Isolated species of course exhibit puzzling deviations in this respect. The Acacia (*Robinia Pseudacacia*) develops its flowers in Southern Italy before its leaves, and when the acacia trees are already in full bloom their foliage-leaves are still minute and unexpanded. North of the Alps the foliage-leaves everywhere unfold at the same time as the flowers; and yet we always reckon the heat indicated by the thermometer as if it were utilized in an identical manner by associated plants in all stages of development.

Finally, it must be pointed out that certain alterations which are carried on in the interior of a seed or plant during its apparent rest, and which have a great significance for those later phenomena of growth visible to the eye, are completely excluded from observation and registration. If potato-tubers are dug up in autumn and put in a cellar, it seems as if all movements and chemical transformations were entirely stopped in their individual cells. The potato-tuber lies tranquilly resting in the dark cellar, in which a constant temperature of 10° prevails, throughout the winter. Spring arrives; above-ground everything germinates and sprouts from the sun-warmed soil, and we connect this phenomenon with the powerful heating caused by the rays of a more vertical sun. No heat-giving sunbeams reach the cellar, however. The temperature of the air, of the earth, and of the potatoes which have been lying there for months is always the same, 10°—even perhaps now a fraction lower, since according to experience the lowest temperature in the cellar is not reached until the end of the winter. Nevertheless the potato begins to grow and to send out a slender shoot from one of its buds, as if it knew that spring, the proper time for sprouting and growing, had arrived. Why does the growth not begin until now in March? Why did it not commence in December, since external influences, particularly the temperature of the environment, was not in any way different within the cellar then from what it is now in spring? There can be only one answer to the question, which is, that in December the potatoes were not yet equipped for growth. They were only apparently in absolute rest; in reality chemical transformations, the preparation and production of constructive materials, were being carried on in the cells, and in December, January, and February, these were not far enough advanced for the tubers to be able to produce stems, leaves, and roots. Not until now in March are the preparations for development completed, and not until now can that transformation of the constructive materials occur which is outwardly manifest as growth. The organic compounds, contained by the cells of the tubers in autumn, were not fit for the formation of stems, leaves, and roots, even under the influence of a temperature of 20°. All these processes require, therefore, a definite period of time, and this can neither be replaced nor sensibly shortened by a rise of temperature.

In the underground bulb of the Snowdrop (*Galanthus nivalis*) the rudiments of the leaves and blossoms of the following spring are already formed during the summer, and at the end of September all portions of the future flowers can be recognized between the enveloping sheaths and bulb-scales. It might be thought an easy matter to force this bulb by raising the temperature and

moistening the surrounding soil, so that we might have the Snowdrop blossoming even in November. But very many experiments have shown that bulbs so treated, although they develop leaves and an inflorescence, do not properly develop their flowers, and always perish prematurely; while four months later the growth of the leaves and flowers takes place easily and quickly at temperatures which are not much above zero. And in many root-stocks, in most buds of branches above the ground, and in numerous seeds and spores, the same thing occurs as in tubers and bulbs of which the Potato and Snowdrop have been selected as well-known examples. How many plants there are which blossom early in the spring, ripen their fruits in the early summer, and whose seeds, being detached from the parent plant in the height of summer, lie scattered on the ground! Although the soil in which they are imbedded is damp and sufficiently warm, and although all the external conditions of germination are fulfilled, yet they do not germinate in the same year in which they have been produced. Not until the following spring do the embryos put forth their rootlets, and then usually under conditions apparently much less favourable than those of the previous summer and autumn. These seeds are not yet ripe, or rather, perhaps, they are not yet capable of germination when they fall from the parent plants. The materials contained in their cells must first pass through a process of transformation before they can promote the development of the embryo, and this transforming process can in no wise be hastened by increased supplies of heat and moisture. In many large seeds, as, for example, those of hazel, beech, and almond, this difference between seeds just fallen from the tree not yet capable of germination, and the seeds which have been mellowed and can germinate, may be easily perceived in their consistency, taste, and smell. The phenomenon here described is found in a specially remarkable manner in the fruits of the Water Chestnut (*Trapa natans*). If in autumn water-chestnuts just ripe be placed in water, and the temperature of the water be kept through the winter at 15° C., the rootlets of the embryos will not emerge until the coming spring, and not then on account of a higher temperature, but at the same temperature to which they have been continuously exposed for six months. If the temperature of the water be raised to 20° the growth of the rootlets is not accelerated, and the increased temperature cannot become effective as an incitement to growth until after the seeds have been suitably prepared for a period of six months. Gardeners say that such seeds must "mellow" and "ripen after gathering", and they have indeed hit the mark with this latter expression. Some spores also must mellow and ripen for a much longer time. Many, of course, germinate immediately after their detachment from the parent plant. The so-called resting spores, however, always pass through a quiescent period, whose duration usually can be determined with great accuracy and may be shortened a little by altered external influences. Very remarkable is the fact that in the seas of tropical regions, whose waters possess the same chemical composition, temperature, and illumination from one year's end to the other, certain species of red seaweeds develop in March, others in June, and others again in October. In these instances all grounds for an explanation are

wanting. It can only be stated with certainty that the increase or diminution of heat does not take any part in this remarkable periodicity. It would, however, be going too far to assert of all species that the resting period, normally observed by them, could not be shortened by external influences, especially by rise of temperature. Many seeds, such as those of cress, mustard, barley, and numerous so-called weeds, which appear as unwelcome guests on cultivated land, have no resting stage, germinate at any season if they are supplied with the necessary moisture; and the warmer the soil the more rapid is their development. It is also well enough known that there are plants which, to use the language of gardeners, may be "forced". Tulips, Lilies of the Valley, and Lilac, whose resting period lasts in Central Europe from the ripening time of the seed in summer until the spring of the next year, may be forced even late in autumn if planted in a greenhouse in warm, damp soil, soon after they have ripened their seeds and have begun to rest. Under these circumstances they produce their flowers even in January, and in these plants, consequently, the materials manufactured in the previous summer may be used as constructive materials for growth almost at once. I remember once drawing the shoot of a Clematis plant rooted in the open, after it had lost its foliage in the autumn, through a narrow crevice 3 metres above the soil into the interior of a neighbouring hothouse. Leafy shoots were developed from the buds of the upper portion thus warmed even in December; while the lower portion of the same plant, situated outside the hothouse and surrounded by cold air, was still frozen. In this plant also, the materials manufactured in the summer could be used as constructive materials as soon as ever they had been deposited in the reserve storehouses.

The same must indeed be the case in those plants which bloom normally in the spring, but yet often in years characterized by particularly mild autumns, burst open in October; the buds destined for the next spring thus sending out fresh leafy shoots and blossoms twice in the same year—for example, many apples and horse-chestnuts, violets and strawberries, many primulas, gentians, and anemones.

Although it may be doubted whether the constants hitherto computed can be taken as an accurate expression of the heat consumed by plants for growth in their various stages of development, nevertheless their value must not be under-estimated. Comparisons of results obtained in various places by the same methods, with the same instruments, and on the same species, will without doubt yet lead to many interesting conclusions. The determination of the commencement of the various phenomena of development, the determination of the unfolding of the foliage and flowers, of the ripening of the fruit, and of the autumnal leaf-fall—at as many stations of observations as possible—is not only a highly attractive problem in itself, but is also of great scientific value; and this no less in its bearing upon the life of plants generally, than upon the geography of plants, since the barriers which confine plants in their distribution can be in great part explained by the fact that the species in question are unable to complete their annual cycle of development on the further side of the boundary. Finally, also for climatology, since the yearly process

of development, in many cases, much more clearly exhibits the climate of a district than the readings of instruments erected in the places in question. The so-called phænological observations, that is, the determination of the awakening of nature at the close of the winter, or at the end of the summer drought, the ascertaining of the times at which growth and blossoming reach their maximum, and the fixing of the period at which the organism, on account of the unfavourable external conditions, falls into a winter or summer sleep, are consequently of interest even if we are unable to reckon the heat constants for the commencement of these phenomena. The results of such phænological observations have been already made use of repeatedly on pp. 519 and 525, and it has been there shown how valuable these may be in questions concerning the relations of heat to growth.

We cannot close this chapter without touching upon two valuable results of phænological observations, although only in passing. The following tables gives first of all a view of the retardation of vegetative development with increasing latitudes in Europe in the spring.

Comparisons with Lesina in the Adriatic Sea, 43° 11′ Nor. Lat., 16° 40′ East Long.

North Lat.	Places between 0 and 10 Meridian.	Retardation in days.	Places between 10 and 30 Meridian.	Retardation in days.	Places between 30 and 45 Meridian.	Retardation in days.
48–49°	Paris	43	Pressburg	58	Sarepta	66
50–51°	Brussels	50	Prague	59	Kiew	68
52–53°	Osnabrück	63	Warsaw	65	Orel	79
59–60°	Christiania	86	——	—	Pulkowa	100

As the starting-point in the comparison we choose the Island of Lesina off the Dalmatian coast, because there the climatic conditions lie midway between those of places situated in the same latitude in Western Oceanic and in Eastern Continental Europe. The stations of observation, situated not more than 300 metres above the sea-level, which are here compared with Lesina, have been arranged in three columns —a western between 0 and 10 meridian, a central between 10 and 30, and an eastern between 30 and 45. Reviewing the retardation due to the increasing latitude with regard to Lesina, we have the interesting result that the retardation in the column of the eastern continental stations is from two to three weeks more than in that of the western column. Thus, when in Paris many spring plants are in full bloom, vegetation on the Russian steppes (Sarepta), at the same latitude, is still deep in winter slumber, and does not reach the same stage until 23 days later.

In a second small table inserted on next page, very remarkable results are given with respect to the blossoming of the same species in Western Europe and in Eastern North America.

Here those American and European stations are placed side by side in which the blossoming of the same species occurs simultaneously, and hence the comparison shows that the geographical position of these places differs by about 8–10 degrees of latitude; so that, for example, in New York (which has the same latitude as

Naples) plants blossom at the same time as in Marburg, situated 10° further north.

Stations at which Spring Plants blossom simultaneously.

North America.	Geographical Latitude.	Europe.	Geographical Latitude.	Difference of Latitude.
New Albany	38° 17′	Dijon	47° 19′	9° 20′
Sykesville	39° 23′	Kremsmünster	48° 30′	9° 07′
Belle Centre	40° 28′	Heidelberg	49° 28′	9° 00′
New York	40° 42′	Marburg (Hesse) ...	50° 47′	10° 05′
Germanstown	42° 80′	Antwerp	51° 13′	8° 33′
Baldwinville	43° 40′	Utrecht	52° 03′	8° 90′

3. ULTIMATE STRUCTURE OF PLANTS.

Hypotheses as to the Form and Size of the Smallest Particles employed in the Construction of Plants.—Visible Structural Activity of Protoplasm.

HYPOTHESES AS TO THE FORM AND SIZE OF THE SMALLEST PARTICLES EMPLOYED IN THE CONSTRUCTION OF PLANTS.

When anywhere within the limits of a flourishing town buildings are raised in great number and quick succession by the skilful hands of men, it is said that the houses grow up with astonishing rapidity from the ground. In the same way the growth of plants is appropriately compared by botanists with the erection of human habitations. In this book the latter comparison has already been made as occasion offered, and, even at the risk of repetition, I must again make use of the simile here in discussing the building up of plants.

As in the erection of human habitations, so in the production of the plant structure, it is a question of providing a home for living beings, of securing this home against injury by weather, and other dangers which might terminate the existence of the inhabitants. At the same time the inhabitants in these settlements must be able to take in food from the exterior, breathe, work up the food-stuffs, and extend themselves further. Where very numerous portions of protoplasm live, associated together in a plant in social union, and where corresponding to this a division of labour has occurred, the whole structure becomes naturally divided up into open spaces where there is no lack of air and light, into contrivances for ventilation, into mechanisms for conveying gas and water, and into chambers for storing up nourishment; in short, it is a question of varied mechanisms within and defences without, of the ensuring of strength throughout the whole structure, and of the necessary supporting framework for the individual parts. Each part occupies a position corresponding to the demand upon it; the light-requiring parts are exposed to the sun's rays; the mechanisms for conveying

gas and water begin and end in the manner best adapted to the given conditions; while the pillars and beams are placed where something has to be protected, borne, or prevented from breaking down.

Such structures, just like the buildings produced by the hand of man, convey the idea of fitness of means to ends. Indeed, they often surpass mere human creations in the suitability of their arrangement. It can hardly be invariably said of man's designs that they are carried out in a way completely suited to the requirements of the case; while no plant lives and maintains itself which is not adapted to the given conditions of life in the most advantageous manner. The most remarkable thing about it is that this adaptation in plants is not produced directly by external influences, but that rather the individual portions assume the most suitable form and position, even in their first rudiments and very early stages of development; that is, at a time in which the forces acting outside the plant can have no considerable influence in directly moulding its form. Such an adaptation presupposes, however, a law of form; in other words, a plan of construction, a plan concerning the division of space best suited to the future division of labour, a plan of the most advantageous construction of the whole framework, the most suitable position of the conducting and ventilating mechanisms, and much besides, which will benefit the plant in the future.

This supposition being forced upon us, the question arises as to whether it is correct to speak of a constructive plan in plants. In the sense in which we speak of the constructive plan of a house, certainly not. Plants are not built according to a plan devised by themselves, but their organs receive their definite form, as if according to a prescribed law, from inward necessity, like the crystal whose shape is dependent upon and founded in the chemical composition of the fluid from which it is formed. But just as we can speak of the plan and elevation, of the symmetrical arrangement, even of the plan of construction, of a crystal, equally well can we speak of the plan of construction, or, if we prefer it, the law of form, of growing plants. The plan of construction is given and traced out for every plant by its specific constitution, and so far every species has its own plan quite independently of the external influences which it follows, indeed, is compelled to follow, as long as the constitution is not altered.

But by specific constitution we do not merely understand the chemical composition, the definite number of atoms, and their characteristic grouping into molecules. We understand further the union of molecules in definite groups of a higher order, which must be regulated in the plant body just as in the body of a crystal. This arrangement of the molecules is characteristic, we must suppose, for every species of plant; further, we must believe that the substance which is associated with the growth of the molecular groups, already present, is always subordinated to the laws of symmetry prevailing there, and that this grouping is not only specific, but also constant and invariable.

When we speak of crystals, we do not mean to say that the processes in question in them and in plants are identical. It is much more probable that there is

a fundamental difference between the construction of crystalline bodies and plant bodies; that this very difference is bound up with the distinction between inanimate and living structures, and that especially are the organized parts of plants fitted by their characteristic structure to those movements which appear to us as life.

Molecules, united in the growth of crystals, admit of no further insertion of plastic substance, of no rearrangement and transformation, of no addition of new molecules between those already present, as is the case with the molecules of living organized bodies. When the molecules of water penetrate into a salt crystal, the molecules of salt separate from one another, and break away, so that we have a disintegration and solution of the crystal, and not its further development. The crystal, moreover, never shows at any time those displacements and movements of the smallest constructive particles which characterize the living organized parts of plants, which in the aggregate we call life. Crystals, therefore, cannot be considered as organized bodies; they are not directly concerned in the phenomena of life, and form no object susceptible to the influence of that specific natural force which we call vital force. They are not, and will never be living, just as they cannot die.

The analogy between the structure of crystals and of plants consists only in the fact that in both cases the grouping of the molecules cannot proceed irregularly, but must always follow definite laws of symmetry. In both cases the external visible form of the finished structure is the expression of a particular and specific grouping of the molecules, and of molecular aggregates known as *micellæ*.

Many attempts have been made to glean some idea of the actual shape of these groups of molecules or micellæ, the bricks—so to speak—of which the plant is constructed. That the hypotheses brought forward are very divergent is not surprising when we remember how few are the data of actual fact that have been observed, and how readily these data admit of varying interpretation, and how full a scope they offer to the imagination of the investigator.

Not long ago the idea found almost general acceptance that micellæ were crystalline in form. In many cell-walls, and especially in certain Desmidieæ, very regular systems of striæ were observed, which ran off into three dimensions of space, and strongly resembled the striæ connected with the cleavage planes of certain crystals (*e.g.* of calc-spar). Since these, and generally all cell-walls, light up the dark field in the polarizing microscope, that is to say, appear doubly refractive, the assumption was supposed warranted that the cell-walls and other organized substances consist of crystalline doubly refractive micellæ, which lie loosely but in regular arrangement next one another. It was imagined that every micella was surrounded, when moist, by an envelope of water, and that on drying, the micellæ came into mutual contact. But later researches have shown that the double refraction can be produced by pressure and strain in substances which do not normally exhibit this property, and that the refraction in the polarizing micro-

scope is not always indicative of the crystalline nature of micellæ. The striation is brought about by dissimilar chemical constitution and unequal quantities of water in the successive strata of molecular groups, and may be present, equally well, where the groups of molecules do not possess crystalline form. Moreover, the results which have been obtained by the so-called carbonization or pulverization of the cell-walls goes against the assumption of crystal-like micellæ. By treating with sulphuric acid, heating up to 60°–70° C., and then operating with hydrochloric acid, the cell-wall is broken up into extraordinarily small fragments, exhibiting parallel striæ and frequent clefts; and these often subdivided into short, very fine filaments, which filaments break up by pressure into granules imbedded in a homogeneous gelatinous matrix. A definite geometrical crystalline form cannot be demonstrated in this ground-substance. Moreover, the granules are not bounded by plane surfaces and rectilineal edges, and have no resemblance to the smallest visible portions of crystals. All the observations obtained by this class of experiment tend rather to show that the granules are grouped into filaments, or lamellæ, or both, that they are joined together by extremely delicate protoplasmic threads, and that the cell-wall possesses a reticular structure. If these granules and filaments are not themselves the micellæ, but groupings, rather, of a higher order, still their outlines in no case suggest the forms of crystalline micellæ. The idea that the micellæ possess a reticular form was corrected much earlier. If the same rule which prevails in the grouping of the molecules into micellæ would also hold in the association of micellæ into groups of high order, and ultimately into bodies which are in their outline recognizable by our senses, then one might hope to derive the form of the micellæ, and even the form of the molecules themselves, from the form of the smallest visible portions of the plant. This supposition would lead to the conception of reticular micellæ and reticular molecules in the organized parts of plants. It is, however, very noticeable that all researches concerning the form of the smallest visible elements of protoplasm point to a reticular structure. In the dry coating of the so-called plasmodia of myxomycetes, which contains no cellulose, but consists of protoplasm (in which are deposited crystals of calcium oxalate), for example, in the plasmodium of *Leocarpus fragilis*, it is seen that the entire papery skin consists of twisted threads extending in all directions, which anastomose in a reticular manner, and that the meshes of this net-work are filled with a highly refringent substance.

In the hyaline ectoplasm of the living protoplasm which inhabit the cell-chamber, very fine threads have been observed lying side by side, and if this protoplasm is displaced and killed by alcohol, it can be ascertained by the aid of colouring matters that the whole cell-body is built up of very minute threads connected into a net-work, and that the meshes of this fine net-work are filled with a fluid substance. Within the threads are to be seen, however, corpuscles arranged in rows, which have received the name of *microsomata*.

The whole protoplasmic cell-body, including the cell-nucleus, appears generally to possess this same structure, for in the processes which lead up to the division

of the cell we always see therein granules, rods, and shorter or longer, straight and curved tortuous threads, twisted in balls, and anastomosing into net-works, which undergo the most wonderful displacements, as will be described in the following pages.

All these observations at any rate do not contradict the supposition of reticular micellæ; and since the conception of molecules built up from atoms grouped in this manner has not been contradicted by chemists, the hypothesis should find support from this fact. Of course the hypothesis of the net-like form of the micellæ is based upon an assumption, the accuracy of which is subject to many doubts. It is questionable whether the same rule always holds in all these groupings and connections. Just as pointed crystals often join up into spherical groups, whose construction follows other laws of symmetry than are observed by the molecules of which the individual crystals are composed, so it is always possible that the combination of the micellæ into visible bodies follows other rules than the union of the molecules into the micellæ.

This change in the relations of symmetry, occuring in minerals, gives rise to the idea of the possibility that micellæ may possess a *spherical* shape, that is to say, the highest degree of symmetry which can be imagined in a body. Some form of symmetry must exist under all conditions, and if the crystalline form of micellæ is excluded, then there remains the possibility of *reticular* and *spherical* micellæ.

Although our thirst for knowledge finds but little satisfaction in hypotheses of this kind, still they are not on this account to be held in contempt. The minutest structure of every substance, whose movements appear to the perception of our senses as life, is far too complicated for us to be able to bring it into the scope of our observations on the life of plants; and in order that we may be able to form a clear picture of all these matters, it is better at any rate to imagine the groups of molecules as net-works and spheres than to imagine nothing at all.

Though we may deny to the micellæ a crystalline nature, actual crystals can be produced by many organized portions of plants. Groups of crystals of calcium oxalate (see fig. 123 [4]) are found very regularly deposited in the net-work which forms the pellicle of myxomycetes. Such groups of crystals are also to be found in the cell-membranes of many flowering plants (Cactaceæ, Nyctagineæ, Commelynaceæ, &c.). The carbonate of lime excreted in the cell-walls of Lithothamnieæ, is likewise crystalline. In other cases these excretions and depositions of lime and of silica are not crystalline, but amorphous, which literally means without form. But we must be careful not to be misled by this expression. These substances cannot be conceived of without a definite shape governed by conditions of symmetry, only they are not composed according to the laws of symmetry governing crystals, and the word amorphous should therefore be interpreted here as non-crystalline. It does not lie within the scope of these remarks to enter into details about the hypotheses as to the shape of the molecules and groups of

molecules of amorphous calcium and amorphous silica; but this much must be said with regard to these depositions, that they cannot be looked upon as organized substances.

Here is the proper place to consider investigations as to the *size* of molecules. In these researches, especially for the ascertainment of the size of molecules of gas, very various physical facts offer themselves as data, such as the coefficients of condensation, the deviations from Boyle's law, the variability of the coefficients of expansion, the heat of evaporation, and, finally, the constants of dielectrics. The results differ considerably. For example, the estimates of sizes given for a certain gas by different methods differ from one another far more than those which have been obtained from different gases by one and the same method. But all calculations agree that the diameter of the hypothetically spherical molecules of gas must lie between the hundred-thousandth and the millionth part of a millimetre, and that these limits cannot be overstepped, either above or below, to any great extent even in the extremest cases. A cubic millimetre of gas would therefore contain about 866 billions of molecules, and if the gas were condensed into a fluid, the number in a millimetre would increase to a trillion.

The length of light-waves is of the smallest of measurable dimensions. If the diameter of a molecule is taken in round numbers at the millionth part of a millimetre, this is 700 times smaller than the wave-length of red light, and the diameter of a molecule bears about the same proportion to a millimetre, as a millimetre to a stretch of 2 kilometres. Particles of these dimensions are beyond the conception of our senses; even the highest powers of the microscope are unable to disclose them to us, as is shown by the following considerations. Sheets of gold-leaf are produced, whose thickness amounts to only a hundredth part of the wave-length of light, and which accordingly contain only 3–5 molecules of gold above one another. These gold-leaves are transparent to white light, and this may be regarded as a proof that rays of light penetrate through the chinks between the molecules. Nevertheless this leaf appears as a continuous mass under the best microscopes, and it is not possible to recognize the individual molecules composing it. Under the most favourable circumstances, our microscopes are able to render visible only particles which comprise perhaps two million molecules. Since there are no certain data to enable us to measure how great is the number of molecules from which micellæ are built up, and in what manner the molecules are grouped in them, it would be rash to attempt any conjectures as to the size of micellæ. The possibility of perceiving micellæ with the microscope in their outline and shape, especially those of albuminous bodies, whose molecules are composed of such a large number of atoms (see p. 456) is not to be wholly excluded, particularly since our microscopes are still capable of much improvement. Still, the probability is but a remote one, and as matters stand at present, all conclusions on this subject would be of the nature of theory, in which one uncertain hypothesis has to furnish the foundation for a second, still more doubtful.

VISIBLE CONSTRUCTIVE ACTIVITY IN PROTOPLASM.

Though it is improbable that we shall ever succeed in seeing the micellæ of which the organized living portions of plants are built up, and though all attempts to form a picture of these tiny units are only founded upon conjecture and hypothesis, still we can follow with our eyes the general operations, the constructive and shaping activity of the protoplasm.

This formative activity can be most easily observed in the comparatively large protoplasmic bodies of myxomycetes, in their so-called plasmodia; therefore some of the most striking of these processes will now be briefly described.

The myxomycete *Leocarpus fragilis,* which commonly occurs on the bark of dry, fallen branches of the Pine, forms a viscous yellow mass, looking deceptively like the spilt yolk of an egg. The dead branch is covered by a thin layer of this substance, in which no particular projections can be recognized. Quite late in the evening *Leocarpus* can be seen in this plasmodial stage. During the night, however, it rises up in certain places into knobs and warts, and the whole mass then has a coarsely granular appearance. Towards morning, pear-shaped bodies, supported on thin stalks, are produced from these protuberances, which are now no longer viscous, but exhibit a thin dry pellicle. Within, they have become transformed into numerous hair-like threads, with black powdery spores lying between the threads. *Leocarpus* needs about 12 hours for this manifestation, and if one has the patience to observe the mass shaping itself throughout the night, one may actually see how it rises from the substratum, rounds itself off, forms a skin, and assumes the pear-shape form. *Dictydium umbilicatum* develops its plasmodia in the same way as *Leocarpus.* The light brown, irregular, flowing mass of protoplasm gathers itself up into a round cord, which becomes thickened in a club-shaped manner at its upper end, and then spreads out into a delicate net-work with spherical outline. Between the meshes of this net-work the protoplasm separates out into black powdery spores, which are at the mercy of the slightest breath of wind. The slimy protoplasm of *Stemonitis fusca,* on the other hand, rises up in the shape of numerous closely-compacted strands about 1½ cm. long. Each individual strand is divided into a lower, stalk-like portion, and an upper, thick, cylindrical body. This is at first of slimy consistency, but soon becomes dry and divides into a central axis, from which proceed all round an endless number of very fine reticulating threads which break up into thousands of powdery spores, and at the periphery into a very delicate skin, which later on ruptures and allows the spores to fall out. This entire shaping of the protoplasm, with which is connected a change of colour from white to purple, is accomplished under the eye of the observer in about ten hours. The protoplasm of *Chondrioderma difforme* can scarcely be distinguished from that of *Stemonitis fusca,* and yet how very different is the form which it assumes as a plasmodium. First, it is massed into a round ball, and in this is separated out an enveloping skin of innumerable single slender

threads, and a large quantity of dark spores which fill up the space inclosed by the skin. Soon after, the skin breaks up into stellate projecting lobes at the free apex of the spherical body, and now the dark spores can pour out of the open vesicle.

The protoplasm of *Didymium* shapes itself quite differently, and that of *Clatroptychium* differently again. If we were to exhaust the multiplicity of form which the protoplasm of this group of plants assumes, we should be obliged here to actually describe the shapes of all myxomycetes. The above examples will suffice for the establishment of the fact that apparently quite similar protoplasm becomes, in each species, speedily transformed into a definite structure. It only remains to be noticed that the shape assumed by the specifically different protoplasm is quite independent of external conditions; and that in the same light, with the same degree of humidity, and at the same temperature, under the same glass shade, the pear-shaped *Leocarpus,* and the cylindrical strands of *Stemonitis* develop side by side (for illustrations of Myxomycetes cf. vol. II., fig. 355).

The pellicle which bounds the plasmodia of myxomycetes contains no deposited cellulose, and there is consequently in these plants generally no distinction between the pellicle and the body of the cell. The protoplasm of other plants, however, always provides itself, sooner or later, with an envelope in which cellulose can be demonstrated. Of course, cellulose is often present in the cell-wall only in small amount; thus, in yeast, as well as in the majority of fungi, the main part of the membrane is formed of nitrogenous compounds. Various phenomena lead to the conclusion that by the development of cellulose in the skin, advantages are obtained which are not enjoyed by myxomycetes, with their brittle pellicle built up of firm nitrogenous compounds. The soft protoplasm is better protected against injurious external influences by the cellulose wall, and the whole structure obtains that firmness and strength which are absolutely necessary, especially to plants composed of numerous cells.

Moreover, the cell-wall must not be conceived as always a rigid covering, as a chamber with immovable walls. In many instances it is rather to be compared to the skin of an animal, which adapts itself to each alteration in the shape of the body. In no case is the elasticity of the protoplasm hindered by the surrounding cell-wall. Frequently the cell-wall takes no share in the visible plastic processes of the protoplasm which it incloses, and it usually perishes when the transformations have been completed in the space it surrounds and protects. In many instances, on the other hand, the outline and shape of the cell-wall alter in correspondence with the alteration of the protoplasm inclosed by it.

These remarks had first to be made in order to rightly understand the plastic processes to be described successively as *Segregation, Gemmation,* and *Cell Division.*

In the case of the *Segregation* associated with most of the previously described plasmodia, it is to be pointed out as characteristic that the protoplasm divides within a rigid, enveloping cell-wall into completely separate portions of identical shape, and develops no partitions continuous with the surrounding cell-wall. The inclosing cell-wall stands in no direct contact with the formed protoplasmic

masses. Even when the wall remains, and is not ruptured nor disintegrated, it is separated from the protoplasmic masses by the new cell-walls, with which these have meanwhile surrounded themselves. For every species of plant the number, size, and shape of the bodies arising in the interior of a cell by division are quite definite, though they vary from species to species. In the cell-chambers of some species several thousand minute protoplasmic bodies arise. In others, again, the number is very limited. Frequently, indeed, the protoplasm only splits up into two similar halves. If the number is large, the individual masses are exceedingly small, and can only be recognized when very greatly magnified. If the number is limited, the divided portions are comparatively large. The shape of the structures is exceedingly various. Some are spherical, elliptical, or pear-shaped; others elongated, fusiform, filamentous, or spatulate; some are straight, others are spirally twisted, and many are drawn out into a thread; others are provided over the whole surface with short cilia, others again with a crown of cilia at a particular spot, or with only a single pair of long cilia. The illustration on p. 29 represents the most widely differing forms, without, however, exhausting the wealth of configuration. In the majority of cases the small bodies exhibit active movements, and that even within the cell-covering which surrounds the dividing protoplasm; but sooner or later they come to rest, and then assume another shape, or fuse with another protoplasmic body.

With regard to the further changes experienced by the bodies formed by division, many events may be distinguished. In one, the cell in which the division of the protoplasm has taken place opens, the bodies formed glide out separately and swarm in the surrounding fluid. Often they are concerned in fertilization, and fuse with other protoplasmic bodies in a manner to be described later in detail. If not, they surround themselves with a cell-wall, but do not adhere together, or develop into a cell-colony.

In the Water-net (*Hydrodictyon*), described on p. 36 (cf. fig. 197, vol. II.), the parietal protoplasm of a cell divides up into 7000–20,000 minute clumps which exhibit the so-called swarming movement. At first a definite aim cannot be assigned to these movements, but after a short time the particles appear arranged very regularly in a net with hexagonal meshes. They assume the form of short rods, each of which joins at its poles with two others, being cemented to them by excreted cellulose. Instead of a protoplasmic parietal layer in the cell in question a miniature water-net is now seen to have arisen. This becomes free with the disintegration of the parent-cell; its cells grow and increase in all directions without, however, altering the shape once assumed. The process which is observed in *Pediastrum* (fig. 197, vol. II.), a very small water plant allied to the water-net, is very much the same. Here also the protoplasm of a cell which has isolated itself from the others divides up into small clumps which round themselves off, and swarm about for a short time. Gradually they come to rest, assume an angular form, and arrange themselves so as to form two concentric rings in one plane. Where they come into contact with each other, they excrete cellulose and

thus become connected into a tiny disc. This disc consists of as many cells as there are connected clumps of protoplasm, and presents almost the appearance of a honeycomb. Out of this combination each cell can again separate itself from its companions, its protoplasm can divide up afresh, and generally the whole process described above may be repeated.

The Water-net and the discs of *Pediastrum* develop young nets and discs accordingly, from the divided protoplasm in the individual cells. These escape as small colonies of cells from the space in which they were formed, and here a definite isolation of the young cell-colony occurs. In *Glœocapsa*, on the contrary, of which a species (*Glœocapsa sanguinea*) is represented in Plate I., figs. *n* and *o*, the young cell-groups remain joined together. Each cell always divides up, two and two, into protoplasmic clumps, which surround themselves immediately with a thick cell-wall. The old cell-wall, however, does not disintegrate nor rupture; it does not allow the young cell-colony to escape, but it stretches, and the young and old cell-walls are now seen layered one above another. If this process is repeated many times, protoplasmic balls arranged in pairs are to be seen inserted within a whole system of concentrically stratified cell-walls. A process similar to that just described is observed in the ovules of seed-plants, and has been called, though not very happily, "free cell-formation".

Gemmation is essentially different from the process just described. It is observed in plants both with and without chlorophyll, but is not really frequent in the vegetable kingdom. Its characteristic feature is that the protoplasm at a certain point of the circumference of a cell pushes outwards, and in this way a wart or bud-like elevation of the cell-wall, an actual protuberance, arises which, though at first not very prominent, soon increases in area, and in the end assumes the size and shape of the body from which it was produced. We may distinguish two kinds of gemmation. Either an open communication is maintained between the outgrowth and the structure from which it was produced, and no separation occurs at the place of origin; or, the parent cell is shut off from the outgrowth by a cell-wall which subsequently splits, and the outgrowth is detached from the cell-body from which it arose. Very pretty examples of the first kind are exhibited by the Siphoneæ, especially in *Vaucheria*, illustrated in Plate 1, fig. *a*. The tubular cells appear branched, each branch consisting of a tube ending blindly, and all these branched tubes are in free communication with one another. The entire *Vaucheria* is really only a single, much-branched cell—of course a cell which must be called gigantic in comparison with ordinary plant-cells. Species of the genus *Bryopsis* shape themselves similarly, but in these the outgrowths are much more regular than in *Vaucheria*, the whole cell, branched and thus pouched, almost resembling a moss with axes, leaves, and rhizoids. In the genus *Caulerpa* the cell also produces outgrowths, some of which resemble roots, whilst others imitate the shapes of leaves, reminding one, in some species, of small fern-fronds.

Of the second kind of gemmation yeast may be taken as a type. The shape of individual yeast-cells is ellipsoidal. When the yeast-cell grows, the elliptical

form of the body is retained for a time, and the ellipsoid increases equally on all sides. When it has once attained a certain size, the protoplasm bulges out at a particular place, and a wart-like protuberance arises at the periphery, at first exceedingly small, but gradually increasing in extent, and at length reaching the size of the ellipsoid from which it was produced (*cf.* vol. II. figs. 371 [3] and 371 [6]). To say that the cell-wall of the yeast-cell protrudes or grows out, and that protoplasm immediately enters into the protuberance, is not a correct account of this process. The cell-wall here is only passive: it projects beyond the periphery of the ellipsoidal parent-cell only because it is itself the skin of the protoplasm pushing its way out at that point. From one yeast-cell two outgrowths may arise at different places, and each of them, when it has once reached a certain size, may again form protuberances. In this way the yeast shapes itself into a structure which strongly resembles the Prickly Pear in outline (*cf.* Plate IV. and vol. II. fig. 371 [3]). When the protuberance has grown to an ellipsoid, equal in size to that from which it originated, the slightest pressure is sufficient to disconnect the two, and to separate the individual members of the irregular opuntia-like chain. Even without any external stimulus the cells separate, as may be well observed in brewers' yeast (*Saccharomyces cerevisiæ*), which of all the species of yeast has been most investigated.

The formation of yeast by the development of a cell-wall as a partition between two adjoining cells reminds one of the *division of cells* which has now to be described as the third formative process connected with growth. The division of the cells is always accomplished in the following manner:—The protoplasm, inclosed in its cell-wall, develops a partition in its interior by which it becomes divided into two halves, and the cell-space into two compartments or chambers. In some plants the sister-cells produced in division separate from one another, the partition-wall becoming completely split, but in most cases the neighbouring cells remain connected, and then in each of these the same process is repeated; in this way arise multicellular structures, that is, aggregates of cells.

A separation of the two cells arising from a division, due to the splitting of the intervening wall, is observed in the Desmidieæ, those small green aquatic plants, of which two species are represented in Pl. I. figs. *i*, *k*. Although the Desmidieæ consist only of a single cell, their multiplicity of form is considerable. We have cylindrical, semilunar, tetrahedral, stellate, and disc-shaped forms in inexhaustible variety, often occurring in a restricted area, and forming a gay assemblage like the various herbs growing in a meadow. The cell of each species, however, adheres with wonderful tenacity to its plan of construction, and always develops only to a definite size. When once this size is attained, and after the cell has remained unaltered in form for a time, a noticeable change begins to take place. The central portion of the cell (which is constricted in all species) quickly elongates and expands. The protoplasm then develops a dividing-wall, and two cells are now produced from the one. These remain connected for only a little while; the intercalated cellulose wall splits; the two cells separate, and each forthwith assumes

exactly the shape which the parent had possessed. These elegant desmids claim our interest because although their wall is composed principally of cellulose, and is comparatively thick, it has a determinate outline, and in this, and in its protuberances, and, generally, in its entire shape, it is governed by the living cell-body which has formed it. If such a desmid-cell extends in length or breadth, if it bulges out in one place and remains constricted in another, this is caused only by the activity of the protoplasm, which shapes and transforms the body in accordance with the constructive plan of the species.

The continued connection of the cell-couples produced by division, and the origination of extensive cell-aggregates by the repeated formation of partition walls, is much more usual than their separation. No less than five different modifications may be distinguished of this process, which is connected with the construction of so many plants.

In the green aquatic filaments, of which two species (*Zygnema pectinatum* and *Spirogyra arcta*) are illustrated on Plate I. figs. *m* and *l*, a wall may be developed by the protoplasm of each cell, which is first formed as a ring-like band on the already existing cell-wall, and resembles the diaphragm in the tube of a microscope. Gradually from this circular band a completely closed partition-wall is produced, and the single cell becomes divided into two. In each of these cells this process may be repeated, and thus in a very short time may arise a row of four, eight, sixteen, &c., cells. These remain connected with one another, and the whole row constitutes a cylindrical tube divided up by numerous transverse walls. If the single cells are much swollen at the sides, the row of cells has the appearance of a string of pearls. The intercalated partition-walls in these plants are all developed parallel to one another, and are placed at right angles to the axis of the cell-filament.

The fact of these intercalated partition-walls being parallel distinguishes this process from another, which is characterized by the fact that the insertion of partition-walls occurs in two dimensions of space. In this case neither partitioned tubes nor strings of pearls arise, but groups of cells arranged in one plane, which are plate-like in appearance, and, to the naked eye, look like membranes or leafy structures. This kind of structure is often shown by marine algæ which grow on stones. If all the cells adhere to the substratum, as in *Hildenbrandtia*, the outline of the plate is more or less circular, and green or red patches are to be seen on the stone, which continually increase in size without altering their general form. In this case there is no obstacle which could restrict the circular shape of the cell-plate. If, on the other hand, only some of the cells adhere to the substratum, while the others rise up from the stone, so that the whole floats in the water as a thin film (only attached to the substratum at one point), then the further development is unsymmetrical. It is suppressed towards the substratum, and the whole layer usually has a fan-like appearance.

If the arrangement of partition-walls in a cell occurs in three dimensions of space, a tissue is then formed. The tissue-body developing most regularly in this

manner is such as is exhibited by *Sarcina ventriculi*, a vegetable structure which will be presently treated of in detail. Here the eight daughter-cells produced from one cell appear so connected with one another, that they present, taken together, almost the form of a cube (*cf.* vol. II. fig. 372 [10]). One cell always comes to lie in each of the eight corners. Structures of such regularity are of course rare. Usually manifold variations take place. In the so-called pollinia of orchids hundreds of daughter-cells are developed by repeated division, grouped into small balls which again form a large, irregular, clumpy mass. It frequently happens that a group of cells, which increases at the periphery in three dimensions of space, in consequence of the intercalation of division-walls, does not exhibit, as would have been expected, a symmetrical growth on all sides, but increases chiefly in one of the three dimensions. This form, which is specially observed in stem structures, depends upon the development of a so-called *apical-cell*. By this is meant a cell which forms to some extent the apex of a cellular body constructed on a horizontal base. By the insertion of a partition-wall a chamber, a so-called segment, is formed from the lower half of the apical-cell. While fresh divisions are being accomplished in this segment the upper half of the apical-cell again grows up to the original size; and if one did not know that a segment had been cut off from it a short time before, it might be thought unaltered with regard to size, position, and shape. After a little time the segmentation just described is repeated and forthwith it again recovers from the loss, and attains to its original size. Thus the apical-cell cuts off one segment after another at the base, and builds a pedestal on whose highest point it enthrones itself. The apical-cell comes in this way to be raised always higher and higher, as it were pushing its way through the surrounding air or water at the head of a group of cells; and to a certain extent the direction of growth, as well as the internal tissue of the groups of cells cut off from the apex, are ruled and ordered by the processes of division carried on within it.

This results from the fact that the position of the segments separated from the apical-cell (*i.e.* of the intercalated separation-walls), is always arranged in a definite manner. If the division-wall, which arises in the lower part of the apical-cell, parallel to the base and at the same time at right angles to the direction of growth of the cell, and if the further divisions arising in the repeatedly-divided segments occur in three dimensions of space, as is the case, for example, in the Characeæ, then the whole plant is built up in stories. The chambers of the lower story are produced from the first segment cut off from the apical-cell, those of the next higher story from the second, and so forth. The whole structure, however, is terminated above by the indefatigable apical-cell, which continues to divide in the same way as at the commencement of the edifice.

In other cases the separation-walls, which have been intercalated successively in the lower part of the apical cell, take up an essentially different position from that in the Characeæ. They are frequently placed *obliquely* to the direction of growth of the shoot-axis, and the base of the cell is either wedge-shaped or three-sided. It is wedge-shaped, for example, in some liverworts (*Aneura* and *Metzgeria*) as well

as in *Selaginella* (belonging to the family of the Lycopodineæ). Here we have inclined walls formed alternately on the right and left, and thus arise two rows of segment-cells, arranged with regard to the axis of growth like the barbs of a feather on their axis. The base of the apical-cell is three-sided in the stems of horse-tails, most ferns, and mosses. Such an apical-cell may be best compared to a three-sided pyramid, whose sides are not flat but somewhat convex. The side of this cell, which corresponds to the base of the pyramid, forms the free end which is not bordered by other cells, but by the air, or earth, or water; the three other sides, directed towards the base of the growing plant-organ, converge at a point which lies in the axis of growth of the organ. The insertion of division-walls occurs parallel to these three slightly arched sides, and in a regular succession, so that the segments cut off appear arranged like the steps of a spiral staircase. The walls which are afterwards inserted in the segment-cells are partly parallel, partly at right angles to the first-formed walls. On the whole it cannot be questioned that in this building, as in the buildings of men, the walls are intercalated at right angles to one another in three dimensions of space.

In the root-tips of ferns and horse-tails, we also have a three-sided, pyramidal apical-cell, as just described, but the construction is to some extent complicated by the fact that division-walls also arise parallel to that side which corresponds to the base of the three-sided pyramid. The segments so cut off, which divide up again into many cells by radial walls, cover the apical-cell like a cap. This structure, which has been called the root-cap, serves to protect the apical-cell at the root-tip as it pushes its way into the earth, and would otherwise be exposed to many dangers.

In some ferns, and in most flowering plants, two, or even a group of cells are to be found at the tips of the growing stems. Some trouble has been taken to reduce the arrangement of these to three types, but it does not lie within the scope of this work to describe these in detail. That the construction in these cases is extremely complicated, that in many cases it is very difficult, frequently even impossible, to follow and to establish with certainty the plastic processes, does not in the least alter our conviction that the construction of the growing organs in these plants is accomplished according to rule, and that a definite plan underlies the form of every species, which is indicated beforehand by the specific constitution of the protoplasm.

It must also be here remarked, to prevent misunderstanding, that in plants in which numerous organs are developed with various functions, all the growing parts are not formed in the same manner. This, however, is not opposed to the fact that in each species the same constructive plan is invariably adhered to. The directions of the septa inserted in the growing rhizoids, leaflets, and capsules of a species of moss may differ much among themselves, but in each species they are always the same in the various organs. In flowering plants, too, the processes in the formation of the root-cap, the stomata, the pollen-grains, and so forth, vary very much among themselves, but these processes are retained in each species of

plant with great constancy. In the same species the root-cap, stomata, and pollen-grains are always found to be constructed on the same plan. In poppy flowers which had developed two thousand years ago in Egyptian soil, and which were then placed in tombs as ornaments of the dead, the cells of the anthers and pollen are formed precisely as in poppy flowers which grow in our fields to-day. It is important to hold firmly to the fact of this constancy. On it is founded not only the possibility of distinguishing between species of plants, but, generally, the conception of kind or species, to which we shall repeatedly return.

The alteration of shape in the protoplasm and its walls, just described, refers in each case really only to the external contour. Obviously, definite displacements and arrangements in the interior of the living protoplasm lie at the foundation of these alterations, and it is reserved for further investigation to establish these latter as far as they are visible and recognizable. Hitherto the alterations occurring in cell-division in the substance of the protoplasm, especially in the so-called cell-nucleus, have alone been accurately observed, and what has been seen there has already been briefly stated on a previous occasion. This is the place to return to these remarkable phenomena, and to collect together the most important results in a brief review.

Let us look at a cell in which the protoplasm fills the whole interior. A large cell-nucleus is visible in the centre of the cell-body. The protoplasm exhibits when very highly magnified, granules, and fibrils, the latter long and short, curved and straight, knotted and twisted or rolled into balls, and anastomosing into a net-work. This structure appears most plainly, especially the filamentous formation, in large nuclei. The twisted threads there visible have been termed nuclear fibrils. In many instances there seems to be only a single much-twisted thread present in the nucleus. In other instances more are to be seen, and they appear to be distributed with some uniformity in the nucleus, as shown in fig. 138 [1]. The change begins first of all with the division of the nuclear threads; from them are formed numerous short, twisted rod-like, or granular portions, which journey towards the centre of the nucleus, take up a position there corresponding to the equator of the cell-nucleus, which may be compared to a geographical globe (see fig. 138 [2]), and arrange themselves into a plate which has been called the nuclear plate. Soon, however, a detachment again occurs of the constituents of this plate. They separate from each other, each fibril splitting into two, and seek the poles of the spindle (fig. 138 [3]). As they do so the fibrils turn and bend themselves, usually so that those going one way have the form of a ∪, and in the other of ∩. Arrived at the region of the pole, the filamentous portions fuse, contract on every side into a dense skein (fig. 138 [4]), and thus from one cell-nucleus two nuclei result.

A system of very delicate filaments also plays a part in these movements of the elements of the nuclear plate. These filaments, as may be seen in fig. 138 [2, 3, 4,] form a spindle. This spindle arises, not from the nucleus, but from the surrounding protoplasm. The spindle appears to serve the nuclear fibrils for support and guidance in their movements, leading the fibrils to the poles, where they join

together again into two fresh nuclei. After they have performed this function, these spindle filaments have a further and no less important part to play. Almost at the identical place where the nuclear plate was previously to be seen, an accumulation of exceedingly small granules arises, the repeatedly mentioned microsomata; and these are arranged to form a plate, the so-called cell-plate, which ultimately divides the whole cell into two compartments. Apparently these spindle-threads serve also as conductors to these microsomata, and many of the small granules are conveyed along them to the equator. But occasionally they arise there directly, and help to produce the cell-plate. The development of the cell-plate does not seem to be always quite the same in different species, but it is established with certainty that in it cellulose micellæ are always formed, and that the partition-wall produced from them possesses the characteristics of a cellulose wall, that is to say, of a cell-wall. Already it has been mentioned (p. 44) that in

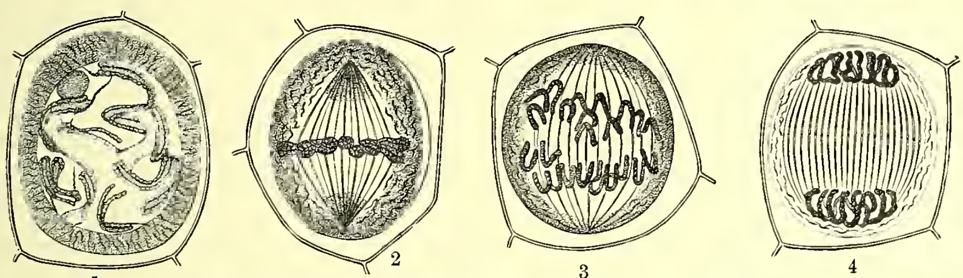

Fig. 138.—Changes in the Protoplasm of the Cell-nucleus during its Division.

[1] The nuclear fibrils distributed through the whole nucleus. [2] The broken-up nuclear fibrils arranged as the nuclear plate. [3] The elements of the plate separating from one another. [4] The same elements forming two skeins at the poles of the spindle. (After Guignard.)

this cell-wall, at least at first, albuminous portions of protoplasm are retained by means of which the intercalated membrane can undergo manifold metamorphoses, and that by them, if required, the communication is maintained between neighbouring masses of protoplasm.

In the cells of those green water-threads known as *Spirogyra*, *Zygnema*, and *Cladophora*, as well as in those of desmids and many other simple plants, the plants never seem to come to an end of this dividing. Each cell continues to grow until it has attained certain dimensions; it then divides into daughter-cells in the manner peculiar to it, and in these the process which has been performed in the parent cell is repeated afresh. This process continues perpetually under favourable external conditions, and an interruption occurs only when there is lack of necessary food, or when the living protoplasm is killed by unfavourable circumstances. In these plants, of which we can enumerate more than a thousand different species, there is thus no distinction into portions in course of formation and those which have been completed, and are no longer capable of development. It is otherwise in large plants in which a division of labour and a corresponding organization have taken place, in those plants whose different members perform different functions. In these, stability of some members is of the greatest advantage, and

accordingly besides the cells which are still formative and promote growth, many others are present which undergo no further changes, whose size and shape is permanently retained, and which have therefore been termed *permanent cells.*

Organically-connected groups of permanent cells are called *permanent tissue* in opposition to the groups of constructive, dividing, and changing cells, the so-called *meristematic tissue.* All permanent tissue is obviously produced from meristematic tissue, and the meristem is ultimately derivable from a single cell capable of division.

The cells of meristems exhibit only very slight variations in form. It is impossible to recognize what forms the permanent tissues produced from them will in time assume. Of four exactly similar meristematic cells, the first may become the starting-point of several flattened epidermal cells devoid of chlorophyll; the second for the formation of a group of green palisade-cells; the third for a bundle of elongated, thick-walled bast-cells; the fourth for several delicate-walled, large parenchymatous cells. It is difficult to explain how this comes about, and we relinquish the attempt to give a full explanation here. Only this much may be remarked, that whilst the stimulus to these metamorphoses comes from outside, and external conditions have a determinative influence on the size of the developing permanent tissue, the shape, outline, and definite configuration which the individual cells in the permanent tissue assume, as well as the arrangement of the various cells in space, are independent of external influences. Just as in a plant the first division-walls assume a position defined beforehand in the dividing apical-cell, the further metamorphoses of the daughter-cells proceed within the limits settled by the specific constitution of the protoplasm, so the transformation of the cells of the meristem into cells of permanent tissue is governed according to a plan of construction peculiar to, and hereditary in, each species.

This law, derived from numerous facts, of the independence to external influences of the constructive plan and character of the cells, seems to be contradicted by the fact that alteration in the outline of individual cells can be produced by strain and pressure. Spherical cells with elastic, flexible walls may be changed by strain into ellipsoids; in consequence of all-round pressure a spherical cell may assume the form of a rhombic dodecahedron, or by lateral pressure, the form of a six-sided prism. In explanation of these conditions it has been pointed out that peas which are made to swell up in a cubical, thick-walled vessel, by pouring water over them, assume the shape of rhombic dodecahedra, because each individual pea is in this way allowed the greatest possible room together with the utmost economy of space. We are again reminded of the fact that the structure of slate-like stones is dependent upon the pressure acting upon the mass so far at least that the planes of cleavage and stratification are always at right angles to the direction of the pressure. But however valuable these facts are in the explanation of the condition of the form of inorganic bodies, they are of little significance to the question in hand. No one will deny that spherical cells on which an equal pressure operates from all sides may assume the shape of dodecahedra, but this form is not

transmitted to the descendants. In the next generation of these same plants it is a group of spherical and not of dodecahedral cells, which arises at the particular place. The latter will, indeed, only reappear if the aforesaid pressures be again exerted.

How little, however, external influences define the form and grouping of permanent cells, is shown by the fact that from one and the same meristem, under the same pressure, the same temperature, and equal illumination, arise in the closest proximity the most different permanent cells; and that, on the other hand, the formation and grouping of these cells is not essentially different when the development of the meristem takes place under wholly different external pressure, or different temperature. We always come back to this important thesis:—the forces operating on plants from outside are only *stimuli* to the formative processes; these latter are accomplished independently of external influences in a manner established for each species, and founded in the specific construction of its living protoplasm.

PLANT-FORMS AS COMPLETED STRUCTURES.

1.—PROGRESSIVE STAGES IN COMPLEXITY OF STRUCTURE FROM UNICELLULAR PLANTS TO PLANT-BODIES.

Though all plants are mortal, they have the capacity of renewing themselves and rejuvenating, so that, in spite of their perishable nature and limited duration, the species now existing on the earth are in no danger of extinction. The rejuvenescence is always effected by means of the protoplasm of a single cell; *i.e.* by a small mass of slimy substance which can only be perceived by the naked eye in the rarest instances on account of its minute dimensions. The largest palm in its rejuvenescence must pass through this unicellular stage exactly in the same way as the smallest of mould-fungi. The only difference is that in large and usually long-lived plants a longer time elapses before this stage is reached, while in small plant-forms many generations may pass away and be replaced in the course of a single year. The protoplasm in the minute rejuvenating cell always grows at the expense of its surroundings, moulds itself in the manner peculiar to its species, and divides when it has attained to a certain size into two or more masses, which have inherited the capacity of dividing afresh.

Each one of these protoplasmic masses is to be regarded as an individual. When the adjacent masses of protoplasm, the result of continued division, remain in connection with one another, as indeed seems to be usually the case, each retains a certain degree of independence; nor, should a severance take place, are they necessarily abandoned to destruction. Under favourable conditions they may, although separated from their companions, enlarge, divide, and continue to grow. In not a few unicellular plants it is even customary for each mass of protoplasm immediately after its formation to separate itself entirely, and, for the future, to live independently. It is remarkable that in most of these unicellular plants a time arrives, *i.e.* the time of pairing, when they again seek each other with the view of uniting; but this period is of short duration compared with the length of the isolated life. Moreover, a definite bond of union has been recognized between the separate individuals produced from one cell. Just as caterpillars which creep out of the eggs laid by a butterfly are seen not to disperse, but to follow common paths and ways, so the swarm-spores of *Sphærella pluvialis* swim together in groups from one place to another, and select a suitable spot for settling down. The

single cells of diatoms and desmids form similar social groups living within restricted areas. We must suppose that here—exactly as in the young brood produced from the spawn of a fish, which swim in company through the water, or in midges hatched simultaneously, which dance up and down in the evening sun—here must be some kind of family feeling which binds the different individuals together, although we cannot fully comprehend these relations between the several organisms.

When the single genetically-connected masses of protoplasm, each retaining its own individuality, can transfer themselves in common from one place to another, like caterpillars, midges, grasshoppers, fishes and the like, the community is called a *swarm*; if, on the other hand, the isolated individuals settle quite close to one another on a substratum, and there take up a definite position for their lifetime, then we speak of a *colony*. The amœboid bodies of some myxomycetes, several unicellular Palmellaceæ, Desmidieæ, and Diatomaceæ, live in swarms; the numerous Siphoneae, on the other hand, as well as the species of the genera *Synedra* and *Gomphonema* belonging to the family of the Diatomaceæ, dwell in colonies (*cf.* vol. II., fig. 373 [2] and 373 [14]). These colonies often attain to considerable dimensions. The Acetabularias attached to stones and mussel-shells at the bottom of the sea, the swollen bladder-like Valonias, the moss-like forms of Bryopsis, and the dusky species of Codium, form, arranged in thousands side by side, very extensive colonies. The Vaucherias, dwelling on damp earth and in cold springs, appear as extensive cushions which cover the ground over a wide distance with a green felt. Besides the swarms and colonies, we have a third form of assemblage, the *cell-union*, in which the genetically-connected masses of protoplasm grow together in a body. This union, again, differs essentially according as to whether the individual masses of protoplasm forming it are devoid of, or are surrounded by, a cell-wall. In the former case they are fused into a mass in which the limits of the single individuals can no longer be recognized, as is the case, for example, in many myxomycetes. The expression "fusion" can here be employed figuratively with the utmost propriety, for indeed the process strongly resembles the fusing of fluid metallic globules into a larger mass, or the fusing of numerous drops of oil floating on the surface of water into a larger drop, in which the contours of the single fused portions are obliterated. It is indeed doubtful whether the fused masses of protoplasm do actually surrender their individuality. Certain phenomena tell rather against than for this view. Thus many myxomycetes form so-called sclerotia, *i.e.* they lose their mobility and pass into a temporary state of rest. The whole mass becomes rigid, assumes a wax-like consistency, and dries up, and the shapeless protoplasm divides into innumerable, clearly-defined, rounded or angular particles. When at the end of the resting period the stiffened mass is to be again transformed into the mobile condition, the individualized particles become fluid and a fresh fusion takes place. The phenomenon observed in the whole series of myxomycetes suggests the idea that the isolated corpuscles in

the sclerotia correspond to the single masses of protoplasm from which the whole mass had previously been formed, and that these have not surrendered their individuality, although their boundaries cannot be recognized in the mass. The unions of fused masses of protoplasm devoid of cell-wall are inconsiderable in number in comparison with the enormous quantity of those combinations in which each portion of protoplasm is surrounded by a cell-wall, by means of which the cohesion of the whole is brought about. The latter are classed as *cell-complexes* or *tissues* and are for the sake of clearness divisible into four groups, which may be distinguished as *rows, nets, plates,* and *masses.*

Its name tells us what a *filamentous* cell-complex looks like. As regards its production, it is to be noticed that the partition-walls, which are formed by the segmentation of its cells, always stand at right angles to the long axis of the cell-filament, and are therefore parallel to one another. The general appearance of this tissue is regulated according to the particular shape of the single cells. If the individual members of the row are spherical, chain-like strings of pearls are produced, such as are found in the Nostocaceæ; if the individual cells are cylindrical, long or short, then thread-like structures arise from their end-to-end arrangement, as may be frequently observed in the Zygnemeæ and the Œdogonieæ. If the cylindrical cells decrease in thickness as the filament increases in length in one direction, whip-like forms arise, as, for example, in the species of the genus *Mastichonema.* Occasionally the single members of the row are tabular, and the tablets are joined to one another by their narrow edges, in which case ribbon-like rows are produced, as in *Odontidium*; or the neighbouring tabular cells are only connected by their corners, in which case the row has a zigzag appearance, as in the genus *Diatoma* (*c.f.* vol. II. fig. 373 [15]).

In the *reticular* cell-complexes the numerous cells are seen to be so arranged that they adjoin one another by comparatively small contiguous surfaces, joining together at two or three, more rarely four, angles of corresponding size. The partition-walls intercalated during the division are not all parallel with one another, but are arranged in more than one dimension of space. Nets may be distinguished as *open* and *closed.* In the former, which may be best compared with the net-work of rivers on a map, the cells only seldom form closed meshes, but start out from one another like the prongs of a fork. Open nets occur very often, especially in the mycelia of fungi, in species of the green Confervoideæ living in water (*Cladophora* and *Chaetophora*) and in numerous red Florideæ. Much rarer are the closed nets with hexagonal meshes, as, for example, those of the Water-net (*Hydrodictyon*) described on p. 36, and the remarkable nets of *Volvox globator*, comparable to hollow spheres, which were considered on p. 37. Open reticular cell-complexes permeate the decayed trunks of trees, the mould of the forest-soil, and the humus of the meadow-ground. Here they exist as saprophytes, or on living plants and animals as parasites; or they are only attached by a few cells to the substratum, and the forked ramifications stretch out from these starting-points like fans and radiate

forth into the surrounding water, as in most water-plants belonging to this category. The closed nets, on the other hand, are never joined to a substratum, but remain floating in the water from which they derive their nourishment.

The *plate-like* cell-complexes are composed of cells arranged in one plane, and adjoining one another so as to leave no intercellular spaces. The partition-walls inserted in the separate chambers during the development of this form are arranged in two dimensions of space, and frequently intersect at right angles. These cell-complexes either form a thin coating on stones or other solid bodies, and then adapt themselves closely to all inequalities of the substratum, as *e.g.* in *Protoderma viride,* which covers the stones and old tree-trunks in mountain-brooks; or they appear as membranes, ribbons, and delicate leaf-like structures, which are attached to the substratum only at one point, and for the rest float freely in the water. This is what occurs in the Sea Lettuce (*Ulva*), and in many Florideæ, as, for example, *Porphyra.* Sometimes the plate-shaped complexes are developed as quite independent, unattached tablets and discs, as in the genus *Pediastrum* (*c.f.* vol. II. fig. 197 [6]). The leaf and ribbon-like forms which float in water are but seldom quite flat; usually they appear much bent, undulated, and pitted; the margin, also, is generally crinkled or slit, and divided into lobes and fringes, and these forms thus furnish transitional stages, half cell-plates, and half cell-nets. In the matter of size, all possible gradations are to be found, from the minute discs of *Pediastrum,* and the small membranes of *Prasiola* flourishing in glacier-streams, up to the Ulvas, living in the sea, many of which grow up into membranes a square metre in area.

Mass-like cell-complexes are those whose constituents adjoin one another in three dimensions of space. Both in transverse and longitudinal sections of their tissues we have at least two, but as a rule several stratified cell-layers. Usually the whole body is elongated much more in one direction than in the others; frequently it has the shape of a solid cylinder or prism, or it forms thick fibres, cords, and ropes. Many remind one of earth-worms, or they resemble the tentacles of polyps and sea-anemones. In many Florideæ, and especially in the brown leathery sea-wracks, these cell-complexes are strap-shaped, or they are contracted into a stalk below, where they are attached to the substratum, and above widen out into leaf-like structures, as, for example, in the Laminarias of the North Sea (see fig. 139), and in many other cases. These strap-like, ribbon-like, and leaf-like structures occasionally remind one of the similar plate-shaped cell-tissues of Ulvaceæ, previously mentioned, but are distinguished from them by the fact that they are always built up of two or more stratified layers of cells, so that a section taken at right angles to the leaf-like structure always exhibits two cell-layers at least. Cake-like and ball-shaped tissues are rarer. As examples of the latter various species of *Glœocapsa* may be instanced, one of which is illustrated in Plate I. fig. n.

In most of these simple cell-complexes the bulk of the cells are shaped similarly.

Usually only the portions serving for reproduction exhibit differences of shape, and these are so subordinate in number and extent that the appearance of the whole is very little altered whether they are present or not. It is of more importance with regard to the general appearance, that most of the simple tissues enumerated

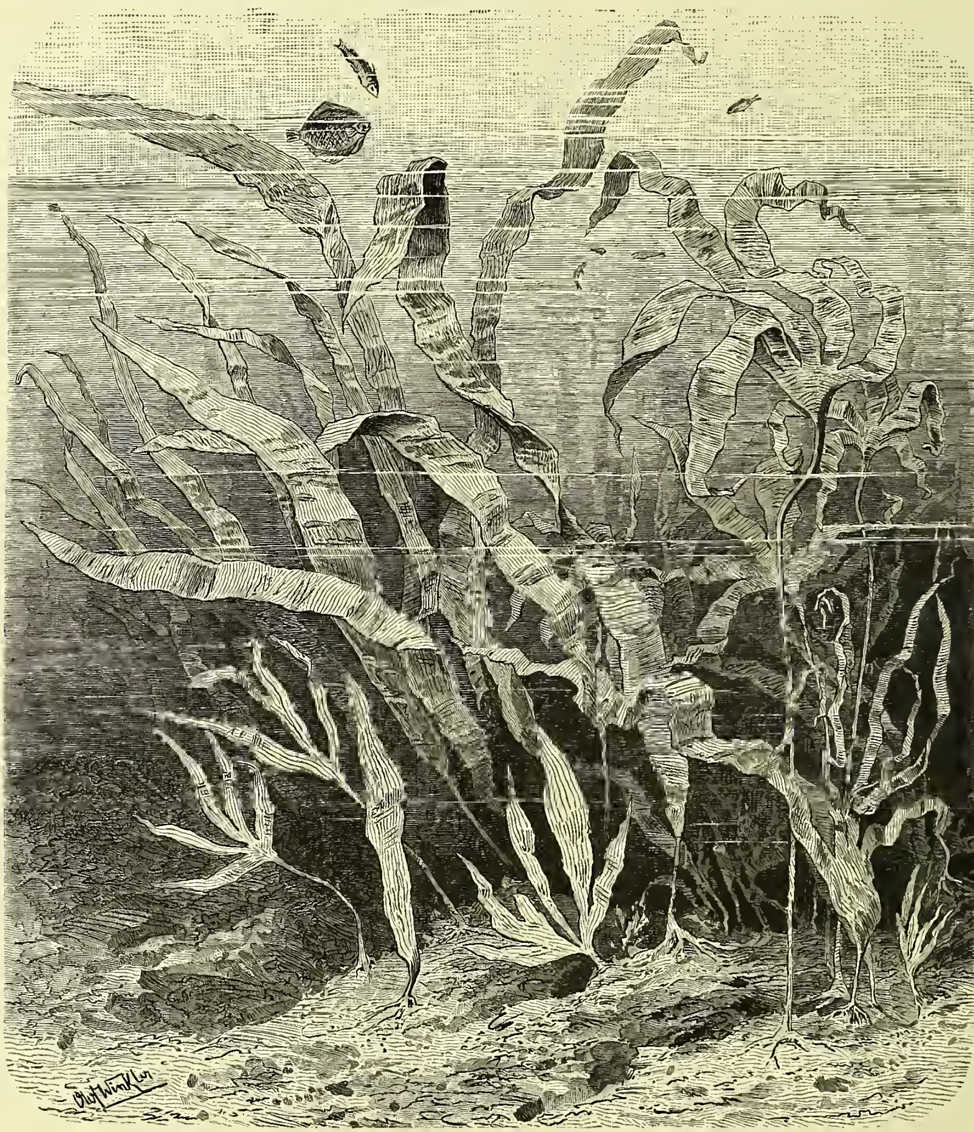

Fig. 139.—*Laminarias* in the North Sea.

multiply and divide without the portions thus produced becoming separate or detached. The nets of *Hydrodictyon* indeed multiply by the formation of daughter-nets within single cells, which then become detached from the parent plant. The disc-shaped plates of *Pediastrum* also multiply in a similar manner, and in this sort of plant whole swarms of cell-complexes are always developed, so that

in the pools where these species grow hundreds and thousands of separate nets are to be found living together within a limited area. But the number of instances of swarm-forming cell-complexes is, however, utterly insignificant in comparison with the enormous number of those forms in which the tissues arising by rejuvenescence remain connected. We call these permanently-connected cell-tissues *systems*; and distinguish between systems of cell-rows, cell-nets, cell-plates, and cell-masses. The arrangement of the individual parts, and the fitting together of the systems is quite irregular, but is defined for each plant-species in the established manner, inherited from generation to generation. The simple cell-tissues which build up an extensive system can be distinguished as separate parts, and may be compared to the members of a body, and even called members of that system. There are, of course, systems which consist of very many simple cell-tissues, and therefore have a much-membered appearance; and others which exhibit only a slight organization, *i.e.* are built up of only a few simple tissues. Setting aside the question of greater or smaller, the kind and manner of connection must be taken into consideration in a general review of the forms of plants, and these systems can be comprehended under two divisions.

The first division comprises those whose members (*i.e.* cell-complexes) are all of similar shape, so that the whole plant-body consists only either of cell-filaments, or of cell-nets, or of cell-plates, or, finally, of cell-masses. These uniform systems are found more especially in plants growing under water, which reproduce themselves by spores, as well as in fungi, and the commonest forms to be noticed are as follows:—first, the clusters of tortuously twisted and intertwined rows of cells, like strings of pearls, such as occur in the Nostocaceæ, the bundles of elongated, straight filamentous rows of the Oscillatorieæ, the flock-like *Scytonema* and other aquatic plants, and the dark cushions of whip-like rows grouped in bundles, as shown in the genera *Euactis* and *Dasyactis.* Among the series of complex systems a particular interest is claimed by those which are produced from the frequently-mentioned hyphæ. When the branched hyphæ, often knitted into meshes, and united into net-works, are crowded together in great numbers, plexuses and strands arise which have exactly the appearance of a cell-mass, but which may be distinguished therefrom by the fact that neighbouring cells, whose sides adjoin one another, are not produced by the intercalation of partition-walls. The fungal hyphæ have a common development and manner of growth; hundreds of hyphal threads which are joined together into a strand or plexus continue to grow at the apices with equal rapidity and in the same direction; they carry out in common the same curves and twistings, often divide into single threads, then reunite, and thus form the most peculiar shapes. The so-called Hercules-club (*Coryne pistillaris*), the strange forms of *Clavaria,* resembling pieces of coral, the Cap-fungi, divided into cap and stalk, the Helvellas and Morels, the very peculiar puff-balls and earth-stars, and many other forms are built up of hyphal strands and plexuses, which, as already stated, are nothing else but conglomerated cell-nets. Systems of cell-plates are more rarely to be met with. This construction is found most

noticeably in the marine *Padina Pavonia*, older species of which are composed of superimposed, thin, leaf-like cell-plates. Systems of cell-masses are found in many Florideæ and especially in the large brown sea-wracks, *Cystosira*, *Sargassum*, and *Fucus*. The separate cell-complexes, which form a system in these plants, frequently assume the form of leaves, and these sea-wracks are occasionally ranked with leafy plants, which will be described later. *Hydrurus* and the Stonewort (*Chara*) are systems of cell-complexes; but while the individual complexes in *Hydrurus* are connected very irregularly, they exhibit in *Chara* an extremely regular, geometrical, whorled arrangement (*cf.* vol. II., fig. 206 [1]).

Following this first division of systems, which have a uniform construction, is the second, in which the body is built up of different kinds of cell-complexes. These are called *mixed systems*. Each member of such a mixed system, regarded by itself, exhibits a simple homogeneous cell-tissue; but the simple complexes are so combined that in one case cell-rows are carried by a cell-plate, while in another case a cell-mass forms the starting-point for several open cell-nets, and so forth. All possible combinations are realized in nature, but none more frequently than that in which a cylindrical cell-mass forms the centre or axis of the whole plant-body, whilst cell-plates or nets are laterally articulated. In many sorts of *Batrachospermum* open nets are seen which are borne on a central pillar of cell-masses; and in a liverwort (*Jungermannia trichophylla*) the same thing occurs, except that here there are cell-rows which proceed from the lower parts of the central mass (fig. 140 [6]). Many mosses and liverworts (*e.g. Hookeria splendens* and *Jungermannia polyanthos*) exhibit a stem-like central tissue which does not carry cell-nets, but single-layered cell-plates. As shown in the illustration opposite, all possible stages are to be seen in moss vegetation between central supports provided with cell-nets, and those with cell-plates; this must be particularly noted here, in order to establish the fact that all classifications and distinctions based upon external forms are really only artificial, and that sharp limits between the various forms do not exist. Still it conduces to clearness, none the less, if we collect together and classify the various forms as well as we can. The mixed systems which are represented by the liverworts, illustrated here, claim an especial interest, inasmuch as they are to a certain extent the prototypes of plant-bodies, *i.e.* of those complex forms which botanists in earlier times alone recognized when speaking of the configuration of plants; these alone were considered, for example, in Goethe's Theory of Metamorphosis.

The *Plant-body* is always membered, and each of its members is composed of cell-complexes of the most varied kinds. In this lies the distinction between plant-bodies and the previously-described forms. The members of a simple and of a mixed system are simple cell-complexes:—cell-rows, cell-plates, and the like. The members of a plant-body are, on the other hand, combinations of cell-rows, cell-nets, cell-plates, and cell-masses. The cell-complexes combined in a member of a plant-body are connected from their first origin. A single cell is always the starting-point for the particular member of the body; this divides; the compart-

ments are again divided, and from the single compartments (*i.e.* cells) originate here plate-like, there mass-like complexes, in this place cell-rows, in that cell-nets; these, however, are not isolated, but remain joined and produce small, wonderfully-arranged structures. The result of this modelling process is therefore a plant-member composed of varied cell-complexes, with a definite internal structure, with definite external contour, and also with entirely definite functions in the economy of the plant. In spite of the variety of shape which plant-members, formed from various constituent cell-tissues, exhibit in the many thousands of plant-species which develop into bodies, they can yet be referred to a few fundamental forms, viz., to the leaf, stem, and root. These members of the plant-body are in

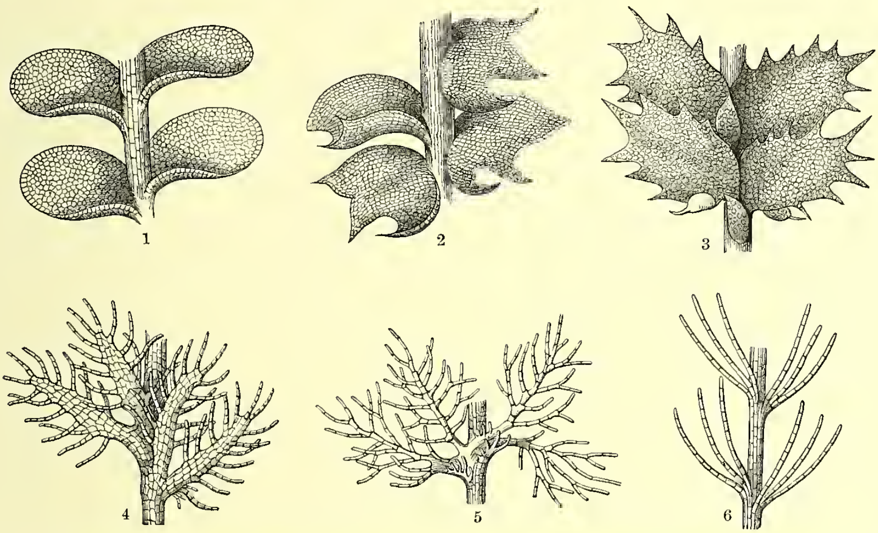

Fig. 140.—Liverworts with Cell-nets, Cell-plates and Cell-rows in various transitional forms.

1 *Jungermannia pumila.* 2 *Jungermannia quinquedentata.* 3 *Polyotus magellanicus.* 4 *Ptilidium ciliare.* 5 *Trichocolea tomentella.* 6 *Jungermannia trichophylla.* (All the figures magnified.)

most cases so arranged that a stem represents the starting-point and support of many leaves and roots. In the simplest form the plant-body appears as embryo and as bud. The latter consists of a very short stem, beset with leaves lying closely above one another, and grows later into a shoot which agrees in structure with the parent plant producing the bud, of which it actually forms a replica. If the young body remain connected with the old, it is called a branch; the branches may again form buds, and these, again, twigs; and in this way originate much-branched plant-structures which often attain to considerable dimensions, and must be regarded as compound. In rare instances the laterally-inserted buds are detached from the body producing them, before they develop further; and these buds, which are known as bulbils, give rise to an independent plant-body. This process reminds one of the swarm formation of cell-complexes which has been spoken of above.

This is also the place to notice the analogy between vegetable and animal

bodies. In polyp-colonies, the individual polyps formed by budding remain in connection with the parent-animal, and behave accordingly like the branches of a compound plant-body. Yet between the parts there exists this remarkable reciprocal relation, that the digestive cavities of individual polyps communicate with one another, and that the liquids acquired by the individuals are at the common service of the colony. This connection of the individual parts by communicating, sap-conducting channels also exists in plant-bodies. We call these conducting channels *vascular bundles,* and have already had repeated occasion to speak of them. They are a peculiarity of *plant-bodies,* and are absent in all other forms of cell-unions, even in mixed systems, many of which have a great resemblance to true plant-bodies, as, for example, the mosses. The difference existing in this respect was the reason for placing the plants in two great divisions in respect of their construction—into (1) the group of those in which vascular bundles are present as architectural elements in their bodies, and (2) that in which this form of cell-system is absent. The former, which are called *vascular plants,* form a natural group; the latter, which are called *Thallophytes,* are, on the other hand, classed quite unsuitably. By "thallus" we understand the most different vegetable structures which are devoid of vascular bundles, that is to say, not only all possible tissues and systems, but also the masses of myxomycetes, even the colonies and swarms of unicellular plants, structures which could not differ more widely in constitution.

It is a remarkable phenomenon that the majority of aquatic plants are devoid of vascular bundles, and therefore, according to the older signification, belong to the Thallophytes; and, on the other hand, that those plants which have assumed the shape of plant-bodies with vascular bundles, belong almost entirely to land-plants. This difference can be more accurately formulated as follows:—plants which throughout their life, or at the time when they absorb nourishment, are surrounded by water, saprophytes which are wholly imbedded in humus, and parasites which are situated entirely within their hosts, absorb nourishment by the whole of their superficial cells. Such structures do not require common sap-conducting mechanisms, penetrating and connecting the several members. Those plants, on the other hand, whose shoots are surrounded by air; which derive their fluid food from the soil, and have to conduct it to the aërial organs, especially the leaves; which finally conduct to the growing parts in a fluid form the organic compounds manufactured in the green tissues in sunlight; such plants require special transmitting mechanisms, and as such, vascular bundles are developed in all land-plants. It is necessary for the stability of the conducting mechanisms that the cells and vessels in question should be lignified, or that so-called mechanical cells, *i.e.* hard bast, should be placed near or in contact with them. Thus it is again made evident that there is a difference between water-plants and land-plants in the matter of rigidity. The numerous submerged plants do not possess woody and bast cells, while these are always abundantly developed in land-plants, and to a greater extent the more the plant in question requires in its natural habitat to

resist strains and bending pressures. Just as we distinguish soft, pulpy animals from such as are provided with skeletons, so also we distinguish soft plants, without wood and hard bast, from hard plants possessing these tissues. I would only point out this analogy in passing, and avoid entering into any further discussion upon it lest thereby misconceptions might arise. In discussing the hypotheses relating to the history of development of the whole vegetable kingdom in the second volume, I shall take the opportunity to return to these analogies, as well as to the relation of the habitat to the structure and form of plants. There the speculations about the evolution of plants on the ground of the comparison here only indicated will receive an impartial consideration. In this place, however, such discussions would be premature, and our remarks might share the same fate as the speculations of the Nature-Philosophers of which examples were quoted on p. 13 of the Introduction.

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2. FORM OF LEAF-STRUCTURES.

Definition and classification of Leaves.—Cotyledons.—Scale-leaves, Foliage-leaves, Floral-leaves.

DEFINITION AND CLASSIFICATION OF LEAVES.

—'T is written—" IN THE BEGINNING WAS THE WORD."—
Already at a stand—and how proceed!
Who helps me? Is the WORD to have such value,
Impossible—if by the spirit guided.
Once more—" IN THE BEGINNING WAS THE THOUGHT."—
Consider the line first attentively,
Lest hurrying on the pen outrun the meaning.
Is it *Thought* that works in all, and that makes all?
—It should stand rather thus:—" IN THE BEGINNING
WAS THE POWER."—yet even as I am writing this
A something warns me we cannot rest there.

Of this speech—which Goethe puts into the mouth of Faust—the naturalist is involuntarily reminded when he attempts to explain terms which popular language from time immemorial has associated with certain ideas. These terms have later gained admission into scientific terminology, and here, once adopted, have gradually been employed to indicate things which no longer correspond to the original current notions. Whosoever introduced into common language the words "leaf", "stem", and "root", little suspected how difficult it would come to be, to say, shortly and exclusively, what botanists mean by these designations—to write down what the man of science understands by a leaf, a stem, a root; nor did he surmise that over the question as to whether or not certain plant-structures should be regarded as leaves, and should be so named, continuous eager strife would rage amongst the learned, and that the polemic writings on this matter, if carefully collected, would fill a book much more extensive than the present one, in which I am attempting to describe the life of the whole Vegetable World.

When a botanist of the 16th or 17th century used the word "leaf" in describing plants, it was exclusively in the sense of the popular acceptation of that term. He understood by "leaf", a flattened outspread structure, such as appears on the branches of trees as a foliage-leaf, green in colour, or, as a floral-leaf, adorned with red, blue, and other colours. Not until the 18th century, and in great part through the influence of Goethe's Essay on Metamorphosis (*cf.* p. 10), did botanists apply the term "leaf" also to the thick fleshy scales of bulbs, to the scales of winter-buds, to many spines and tendrils, to stamens, and to parts of the fruit-capsule. The causes of the movement in this direction were threefold. First, the wish to collect the extremely manifold phenomena synoptically; the struggle to find a simple general law of nature to which the shapes of innumerable single living organisms would conform; further, the similarity of origin—the agreement actually observed over and over again in the earliest stages of development of structures which afterwards become so different; and, finally, the circumstance that occasionally under abnormal external influences, viz., under the influence of mites, plant-lice, and other animals, green leaves are actually formed from the spines, tendrils, stamens, and fruit-capsules. Now, an original or fundamental type of leaf was imagined, of which naturally the shape of the ordinary green foliage-leaf became a standard of comparison. It was represented that the other structures enumerated, which do not agree in their shape, although they agree in their origin with the green leaves, had been produced from these by modification, and that they also must be regarded as leaves, of course as changed or *metamorphosed* leaves. According to this view, the bulb-scales, the stamens, and the parts of the fruit-capsule are metamorphosed leaves, although they do not correspond in their adult form to the idea of a leaf conceived by people who are not botanists.

The struggle after perfection, the gradual refinement of the sap conveyed to the leaves in their first stages, and many other things were at first supposed to be the causes of the transformations. In modern times this metamorphosis is associated with the division of labour, and with the change of function in the members of the plant-body. The green foliage-leaves effect the formation of organic materials from inorganic food in sunlight, but they are not suited at the same time for the protection of seeds or for the manufacture of pollen; nor would they be well adapted as underground storehouses for reserve materials. Consequently certain other leaves of the plant assume shapes better suited to these functions, or, in other words, they are metamorphosed to suit the particular function required of them. We, therefore, do not see green leaves, but stamens developed for the manufacture of the pollen; we do not have green, flattened, outspread foliage as a storehouse for reserve materials in the dark bosom of the earth, but thick, white, fleshy scales. The stamens manufacturing the pollen, the green leaf-blades preparing organic materials in sunlight, and organs, of one and the same plant, fitted to various other definite tasks, are so entirely similar in their origin and first stages, of development, that they are included under a common abstraction, and the word "leaf" has been employed to express it. As in a beehive the adult workers,

the drones, and the queen are of different forms in accordance with their different tasks, as demanded by the division of labour—so the leaves, which agree in their first stages of development, exhibit, in their fully formed condition, another construction in accordance with the function assigned to them. Hence we come to this conclusion:—the variety of the tasks accomplished for the prosperity and maintenance of the whole plant, and the consequent division of labour, necessitate the metamorphosis of the leaves in each plant-body.

From what has been said it follows that a definition of the botanical leaf must be connected with the first stages of development. At the earliest stage each leaf appears as a lateral swelling or protuberance below the growing point of the stem. It arises from the peripheral portions of this region, which are still in a state of active growth. The growth of the leaf is limited, so that in respect of their development, we may say that leaves are *laterally developed members of limited growth, which spring in geometrical succession from the outer layers of tissue below the growing point of the stem.*

In many foliage-leaves we can plainly distinguish a plate-like, outspread, green portion, traversed by lighter veins, the blade (*lamina*), also a firm and stalk-like support for this blade, the leaf-stalk (*petiolus*), and, finally, that portion which connects the leaf-stalk with the part of the stem in question. In many plants this latter portion is widened, grooved, and occasionally provided with a membraneous border, so that the stem is then surrounded by this portion as the blade of a dagger is by the sheath. This part of the leaf has in fact been termed the sheath (*vagina*). Where the leaf projects from the stem there are frequently two outgrowths, one on the right, the other on the left of this sheathing portion. These have generally the form of membraneous scales (see fig. 92 [6]). They are often dilated, as, for example, in the Tulip-tree (fig. 91), and usually fall off when the leaf at whose base they are inserted is fully developed. In other plants they have the form of small lobes or auricles, are coloured green, and are retained as long as the leaf remains connected with the stem. These structures are called stipules (*stipulæ*).

Leaves in which the blade, leaf-stalk, sheath, and stipules are plainly developed, are on the whole less frequently met with than those from which one or other of these portions is absent. Often no trace is to be seen of the stipules. Sometimes only the leaf-sheath is present in the form of a concave, husk-like scale. In other instances the leaf-stalk is absent, and the blade is then situated directly on the stem (fig. 14); or it may happen that the green tissue of the blade surrounds the whole stem like a collar, so that it might be thought that the stem had been stuck through, or had grown through this leaf. If two or more of these leaves with sessile blades arise together, they may be fused into a bowl or cup, being partially or wholly united, and then again it looks as if the stem from which these leaves arise has been thrust through the middle of the united leaf-group (see fig. 56). Occasionally the green tissue of sessile leaf-blades is seen to be continued down the stem in the shape of two green bands or wings. For the forms here only very briefly described, the botanical terms are sessile leaves (*folia sessilia*), perfoliate

leaves (*folia perfoliata*), connate leaves (*folia connata*), and decurrent leaves (*folia decurrentia*), of which terminology this explanation must be given, that in earlier, and indeed even in modern times, the leaf-blade—as the most noticeable part of the leaf—has been in describing plants, shortly called "the leaf" (*folium*).

The classification of leaves with regard to their point of origin from the stem is of particular importance, and in this connection we must first of all distinguish between seed-leaves and shoot-leaves. The former only occurs in the embryo, the latter in all those structures comprised under the term "shoot". The embryo which has developed from the fertilized egg-cell in the embryo-sac—in a manner which has yet to be described in detail—presents in many instances a tissue-body in which as yet no trace can be recognized of a differentiation into stem and leaf, or rather, the embryo, when it leaves the fruit-capsule, is like a stem in which all indication of leaves is absent, *e.g.* in several thousand orchids, the numerous Balanophoreæ and Rafflesiaceæ, species of Broom-rape (*Orobanche*), Winter-green (*Pirola*), Bladderwort (*Utricularia*), Bird's-nest (*Monotropa*), Dodder (*Cuscuta*), and many other epiphytes, saprophytes, insectivorous plants and parasites, as well as many plants living together symbiotically. In the majority of instances, however, a distinct differentiation can be recognized in the embryo hidden in the seed, and one or two leaves may be seen issuing from the tissue-mass which forms the axis of the embryo. These are the *seed-leaves* or *cotyledons*. The short axis or stem-portion from which the seed-leaves originate, and which looks like the pedestal of the cotyledons, is called the *hypocotyl*. At one end of the hypocotyl a tissue-mass is developed, termed the radicle (*radicula*); at the opposite end a tissue-mass named the plumule (*plumula*). (See figs. 141 [1] and 141 [2].) The plumule is situated above the place where the cotyledon, or pair of cotyledons, issue from the hypocotyl. It is the rudiment of a new portion of the stem, which is situated above the cotyledons, and is called the *epicotyl*. The epicotyl thus originates from the apex of the hypocotyl, and the boundary between these two portions of the stem is the place of origin of the cotyledon, or pair of cotyledons.

The epicotyl in the resting seed is frequently only a tiny knob or cone, on which no indications of leaves are yet to be seen. In the majority of instances, however, distinct, although as yet very small, leaflets may be found on it, and where this is not the case swellings sooner or later arise which are the leaf-rudiments. Each short stem-structure, with closely-crowded and overlapping leaves or leaf-rudiments, is called a bud (*gemma*); consequently the plumule is a bud, in fact it is the bud of the embryo, which arises from the apex of the hypocotyl. This bud, at the germination of the seed, elongates; its axis, hitherto very short, stretches; the overlapping leaflets are separated, new leaves arise under the growing-point, and so the bud develops into a structure termed a "shoot" (*innovatio*). The bud is accordingly the primary groundwork of a shoot, and when considering the form of a compound plant-body, special regard should always be paid to the places where the buds originate. The first bud, which is established in every plant-body at the commencement, is situated at the apex of the hypocotyl,

close above the cotyledons. But later on buds are also developed on this primary shoot, and most usually close above the place where leaves arise from the axis of this shoot. Many of the buds elongate and themselves become shoots, and we then say the shoot has formed branches. Some of the buds, however, only undergo a slight extension, and we distinguish between *long branches* and *short branches*, to which we shall return subsequently.

Of special interest to us here are the leaves of these shoots, the whole of which are comprehended under the general term *shoot-leaves*. They exhibit much greater diversity in form than do cotyledons, and this is quite intelligible, since the tasks required from a shoot are much more numerous, and the allotment of various functions to the leaves inserted on the shoot at different heights necessitates a greater wealth of form. But the extraordinary abundance of shapes makes it necessary to group the shoot-leaves according to their origin, their mutual position, and their succession in time. We have long ago complied with this requirement, since we distinguish them as *scale-leaves*, *foliage-leaves*, and *floral-leaves*. Lowest on the shoot we see the scale-leaves. They are developed earliest, and their rudiments are frequently to be seen even in the bud from which the shoot is produced. They generally appear only as the sheathing portions of leaves—as scales devoid of chlorophyll, and exhibit relatively small dimensions. Following these scale-leaves further up the shoot are the foliage-leaves; these arise later, are larger in size, and generally developed with green laminæ directed towards the sun's rays as foliage. Finally, above these, the floral-leaves, which form the termination of the series of leaves growing on a shoot, and take part either directly or indirectly in the production and union of the sexual cells. One and the same shoot does not always bear the three kinds of leaf-structures one above the other at the same time. There are some plants whose shoots never bear foliage-leaves, and it is a very common occurrence for a compound plant-body to develop no floral-leaves on one shoot, and no foliage-leaves on another, while in the *Lathrophytum Peckoltii*, one of the Balanophoreæ described on p. 196, only floral-leaves are formed, and neither a foliage-leaf nor a scale-leaf has ever been seen on this plant.

The leaves, hitherto distinguished only with regard to their succession in age, relative position, and insertion on the stem, must now also be described in connection with the shapes which they assume and the functions which they fulfil. Touching this I cherish the conviction that the special form is always correlated with a special function, and that the recognition of the relation of shape to the performance of work is the highest problem of the science of plants.

COTYLEDONS.

The cotyledons or seed-leaves are borne by the embryonic stem. Their function in the first instance is to provide this organ, as well as the rudiments of the radicle at the one end and the small bud at the other, with food. These portions of the embryo as long as they are still surrounded by the skin-like envelope of the seed—the so-called "seed-coat"—and even still later, when they have burst through these envelopes, cannot at once absorb inorganic food from their environment, and still less can they transform this into organic materials. And yet they require these substances for growth, that is to say, they require materials for the building of the foundation of the plant-body which is to issue from the seed. Only when the radicle has penetrated into the soil and produced its root-hairs, and green leaves have forced their way to the sunlight from the little bud which formed the rudiment of the epicotyl, is the young, newly-settled plant placed on its own feet; henceforth it can nourish itself independently. But up to the moment of this independence it draws its food from a store which is deposited in the seed; it lives on materials derived from the mother-plant, *i.e.* on a supply of starch, fat, and proteid formed by the parent and deposited in special cells for the benefit of the embryo. A fully-equipped embryo is provided with food reservoirs in either of two ways. Sometimes the cotyledons themselves form the storehouse for the food to be consumed later on. In this case the reserve materials are deposited by the parent plant in the cell-chambers of the cotyledon, and when the suitable time arrives, and when the need for them has arisen, these materials are employed in the further construction of the hypocotyl, and of the radicle, springing from one end of it, and of the bud at the other end. In the second case a special storehouse is formed within the enveloping seed-coat beside the embryo. The cells of this storehouse are quite filled with fat and starch and proteid granules. The tissue of this particular store-chamber of the embryo is in most instances composed of cells which have arisen, together with the germ-cell, in the so-called embryo-sac (the large cell in which the egg is produced), and it is then termed *endosperm*. Less frequently this tissue is formed outside the embryo-sac, in the nucellus, and is then called *perisperm*. This distinction is without significance in the processes here to be discussed, and therefore in the following description, endosperm and perisperm are included under the term reserve-tissue.

When the cotyledons themselves form the reserve-tissue, the maintenance of the young plant is relatively simple. The transformation and transportation of the reserve-materials are carried on in the manner already described. In proportion as the radicle of the embryo develops into the root, and a leafy shoot is produced from the embryonic bud at the cost of the building materials conveyed to them, the cells of the cotyledons lose their store of food materials,

and their rôle of nurse is at an end. Often, indeed, the cotyledons take on later another function, but they have ceased to be of importance as reserve-tissue for the use of the developing embryo. In those instances where the supply of food given by the parent plant is not stored up in the cotyledons,

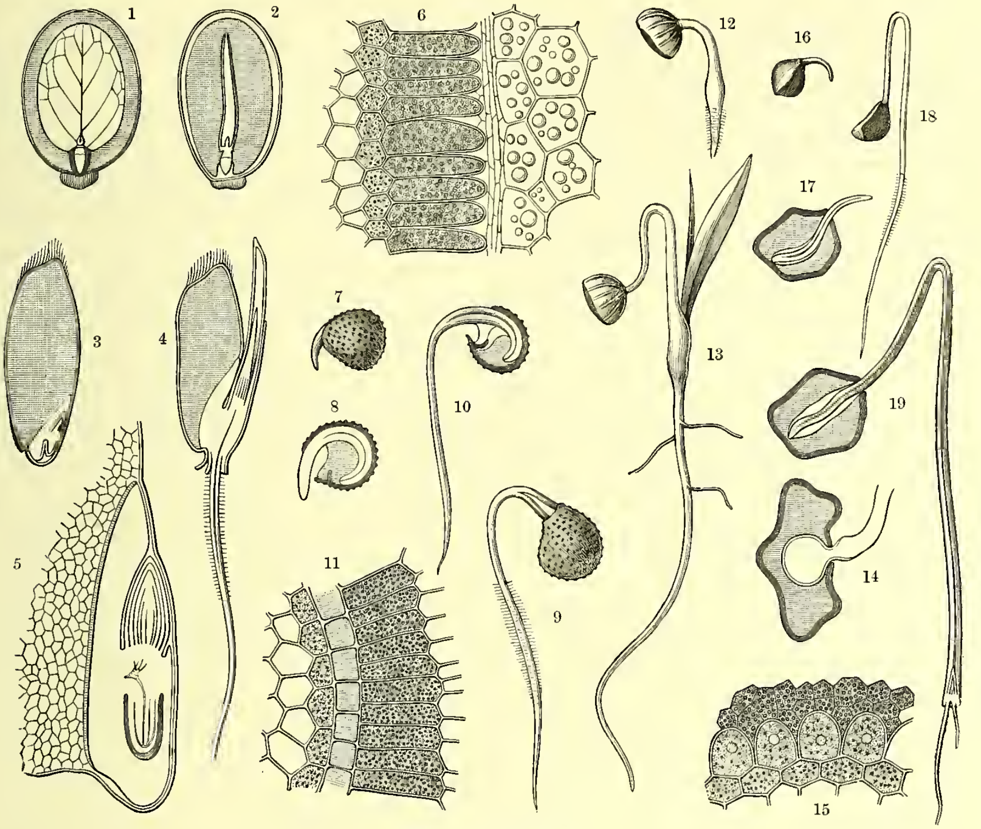

Fig. 141.—Cotyledons.

[1] Longitudinal section of seed of *Ricinus*, parellel to the plane of the embryo. [2] Longitudinal section of the same seed, taken at right angles to the two parallel cotyledons. [3] Longitudinal section through a grain of Wheat (*Triticum vulgare*); × 4. [4] Longitudinal section through a grain of Wheat after germination has taken place; × 4. [5] The embryo with its scutellum in a grain of Wheat; × 80. [6] Absorbeut cells ou the surface of the scutellum of a grain of Wheat; × 210. [7] Germinating seed of the Corn-cockle (*Agrostemma Githago*); slightly maguified. [8] Longitudinal section of the same. [9] Seedliug of the Corn-cockle in a later stage of development. [10] The same in longitudinal section. [11] Absorbent cells on the surface of the cotyledon adjoining the reserve-tissue in the seed of the Corn-cockle; × 210. [12] Germinating seed of *Tradescantia Virginica*; slightly magnified. [13] The same iu a later stage of development. [14] Transverse section through the knob-like end of the cotyledon of *Tradescantia Virginica* embedded in the reserve-tissue; × 10. [15] Absorbent cells on the surface of this knob-like end; × 180. [16] Germinating seed of the Onion (*Allium Cepa*); natural size. [17] The same cut in half; slightly magnified. [18] Seedling of the Onion in a later stage of development; natural size. [19] The same cut through longitudinally; slightly magnified.

but is deposited as a special reserve near the embryo, its nourishment is more complicated.

In this state of affairs the cotyledons have an essentially different function. They serve as agents, and their first task is to take up the building-materials. These have been liquefied in the reserve-tissue, either by changes in that tissue itself, or by the direct solvent action of the cotyledons. They are then conducted

to the growing parts of the embryo. In order to do this, it is necessary that those cells of the cotyledon which adjoin the special reserve-tissue should have the power of absorbing organic compounds from it, and of leading them away. The cotyledons in this respect resemble the suckers of parasites, and, like these, are provided with absorbent cells. In many species, *e.g.* in the Corn-cockle (see fig. 141 [11]) they remain short, form a continuous cell-layer which borders on the special reserve-tissue, and remind one of the absorbent cells of the Bird's Nest (fig. 16 [2]); in others, as, for example, in *Tradescantia* (see fig. 141 [15]), they appear as papillæ, slightly separated from one another at the sides, and resembling the absorbent cells of a Gentian root (*cf.* fig. 16 [1]); again, in other instances, as, for example, in the Wheat (fig. 141 [6]), they increase, at the time of absorption, to ten or twelve times their previous length, and then their side-walls separate from one another so that they are comparable to the absorbent cells of *Cuscuta* (fig. 35 [2]). If the embryo is entirely embedded in the special reserve-tissue, it may happen that *all* its superficial cells in contact with the food-containing tissue, and not only those on the exterior of the cotyledons, act as absorbent cells. If, on the other hand, the embryo only adjoins the reserve-tissue on one side, the absorbent cells also are only developed on this side. The embryo of the Corn-cockle, which is bent like a horse-shoe around the special reserve-tissue (fig. 141 [8]), exhibits, for example, absorbent cells only on the lower side of one of its two cotyledons, which is directed towards the middle of the seed. Frequently only a very small part of the cotyledon possesses absorbent cells adjoining the reserve-tissue, as, for example, in the Onion, where only the end of the cotyledon bears absorbent cells (figs. 141 [17, 18, 19]); or in *Tradescantia*, where the end of the cotyledon presents a knob-like absorbent tubercle (fig. 141 [14]). It is worthy of notice that in many instances where the reserve-tissue is ample and the embryo very small, the extent of the absorbent surface of the cotyledon becomes enlarged during germination. As the reserve materials are absorbed, and the exhausted reserve-tissue shrinks, the absorbing portion of the cotyledon advances. The knob-like termination of the cotyledon of *Tradescantia*, originally of small dimensions, becomes larger in proportion as the reserve-tissue diminishes. The absorbent, hollow, conical or inflated end of the cotyledons of many palms, *e.g.* of the Date and Cocoa-nut Palms, increases in proportion as the reserve-tissue diminishes, presses forwards just as far as the tissue to be absorbed shrinks back, and occupies the space vacated by it (figs. 144 [9] and 144 [10]). A similar relation is to be seen in rushes and sedges. In the embryo of Coffee and Ivy seeds, the cotyledons are at first very small, but grow further and further into the reserve-tissue during the process of germination, till they gradually fill up the whole space in the seed. The cotyledons of umbelliferous plants also behave in a very characteristic manner. The small embryo lies in the seed at the base of the reserve-tissue, and its minute cotyledons project into a space occupied by empty cells, which are however, surrounded by the well-filled cells of the reserve-tissue. Now when

germination commences the two cotyledons grow in length, penetrate through this loose central cell-layer and attach themselves to the reserve-tissue which has to be absorbed.

On the whole it may be taken as correct that the surface of contact between the absorbent part and that which has to be absorbed is greater the quicker the absorption has to be accomplished, on account of the local climatic conditions. Starch is best suited for rapid liquefaction and absorption; fat takes much longer to become changed into a form adapted for absorption; and the transformation of layers of cellulose requires a still longer time. In accordance with this the embryo comes into contact with the reserve-tissue whose cells are crowded with starch (as, for example, in the seeds of pinks, oraches, polygonums, and grasses), presenting a broad surface, or else wrapped with its long cotyledons around the tissue either horse-shoe-wise or spirally. On the other hand, in plants whose special reserve-tissue is principally filled with fat, the surface in contact is much smaller, and the seeds of those plants whose reserve-food consists chiefly of cellulose, *e.g.* those of the Date, usually exhibit only a very limited area of contact between the cotyledon and the reserve-tissue. But in these latter the liquefaction and absorption continue for months, while the same processes in the starchy seeds of grasses and oraches are completed in a few days.

In addition to this first task of the cotyledons, which we have just described, in many instances we have a second function, viz. the extrusion of the hypocotyl and its crowning bud from the interior of the seed-coats. After the formation of the embryo from the parent plant, it remains quiescent for a time, and during this period appears to be protected in the most diverse ways by coverings against the external dangers that might threaten its existence. When a special reserve-tissue is present, the embryo is frequently found embedded in the centre of it, or hidden in its folds. The reserve-tissue is often horn-like, or as hard as bone, as, for example, in the seeds of Date and Coffee, and therefore an excellent protection is provided by this tissue for the dormant embryo. In any case the embryo is surrounded by the seed-coat, which may consist of a single or a double layer. In very many plants the seed is also walled in by a non-dehiscent pericarp (or fruit-covering) and occasionally by other structures. The seed-coat forms an envelope which allows of the entrance of moisture into the interior only by a very restricted opening. It is not flexible or extensible to a great degree, and consequently if the contents swell up and the growth of the embryo begins, then the portion of the embryo designed for further development must either find an exit through the above-mentioned aperture or else it must burst through the husk; or both kinds of escape may occur together.

This process, in which the cotyledons take a very prominent part, is carried on in a manner defined for every species, but in different species by an incalculable variety of methods. Occasionally larger alliances of the vegetable kingdom

exhibit a remarkable agreement, but it also happens that even closely related species of one and the same genus differ considerably with respect to the liberation of the embryonic plant from the bondage of the seed-coat. That some idea may be conveyed of the methods obtaining at germination, eight different cases will be described.

Let us begin with one of the most remarkable cases, viz. with the germination of mangroves, which grow in extensive forests on the tidal swamps of tropical coasts.

The species which I select as example, and whose whole process of development is clearly shown in the figures opposite, is called *Rhizophora conjugata*. A longitudinal section through the pendent flower of this species (figs. 142 [1, 2, 3, 4.]) exhibits two compartments of equal size in the ovary, and in each compartment is discovered the commencement of a seed. After fertilization the corolla and stamens fall off; the calyx remains, and the much-enlarged ovary assumes the form of a stunted cone, whose apex bears two stigmas, now transformed into shrivelled points. If the ovary is cut through longitudinally at this stage of development, it may be seen that one compartment (fig. 142 [5]) with its young seed is atrophied, and the other with its seed has widened and enlarged very much. Within the young seed (which is attached to one side of the originally central wall of the ovary) an embryo can now be plainly distinguished, surrounded by its reserve tissue. Together they fill the egg-shaped cavity, open below, formed by the thick seed-coat. The embryo consists of the hypocotyl, whose free end is directed downwards, that is, towards the point of the pendent ovary, and the cotyledon which forms the upper termination, tubular below, and above not unlike a Phrygian cap. The cotyledon covers like an inverted bell the embryonic bud, which is inserted upon the apex of the hypocotyl. In the lower tubular portion of the cotyledon are numerous vascular bundles which pass down into the hypocotyl and supply it with food. A true radicle is not developed at the lower end of the hypocotyl, and that which was formerly regarded as a root may be more accurately interpreted as the hypocotyl itself. Strangely enough, the fruits of mangroves do not become detached from the branches after the formation of the embryo; nor do they dehisce to allow the seeds to fall out. On the contrary, these germinate while still inclosed in the fruit hanging on the tree. The embryo develops within the seed-coat at the cost of the reserve-food in which it is embedded, absorbing this nourishment by means of the cotyledon. The whole of the exterior of the upper portion of the cotyledon is covered with absorbent cells, and the materials drawn by these cells from the surrounding slimy, gelatinous mass are conducted by the aforesaid vascular bundles to the hypocotyl. Since, in spite of this, the amount of the food stored up does not diminish, and since it is not proportioned to the size of the growing embryo, it may be safely concluded that whatever food is absorbed by the cotyledon, and employed for the growth of the hypocotyl, is continuously replaced by the parent plant.

When the hypocotyl has attained a length of 2 centimetres, the tubular portion

of the cotyledon also extends and pushes the hypocotyl in front of it until the apex has bored its way through the wall of the fruit and come out into the daylight (see figs. 142 [3, 4, 5, 6.]). The hypocotyl now elongates in a month to about 4 cm., and in from 7 to 9 months attains a length of 30–50 cm., and from 1–5 cm.

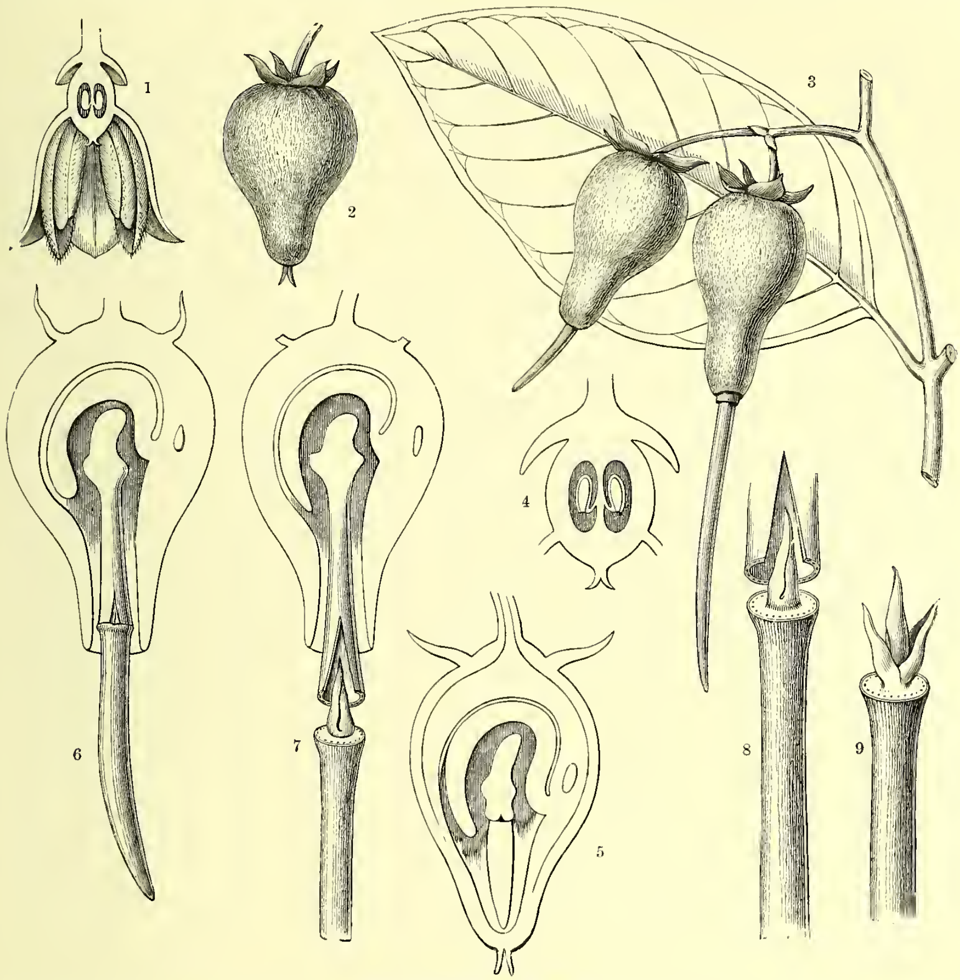

Fig. 142.—*Rhizophora conjugata.*

[1] Flower, cut in half longitudinally. [2] Fruit. [3] Twig with two fruits, whose conical ends have been broken through by the pressure of the elongating hypocotyls. [4] Longitudinal section through the ovary; about twice the natural size. [5] Longitudinal section through a fruit; the cap-like cotyledon surrounded by reserve-tissue; the lower end of the hypocotyl having grown through the seed-coat has reached the lower hollow conical apex of the pericarp. [6] Longitudinal section through a fruit two months later; the tubular sheath of the cotyledon has elongated and pushed the hypocotyl quite out of the pericarp. [7] Longitudinal section through a fruit eight months later. The hypocotyl is separating from the tubular portion of the cotyledon. [8] Part of the same; slightly magnified. [9] Upper end of the hypocotyl with the embryonic bud. The two lowest leaves of the bud are expanding, the two upper are still folded together.

in thickness. It is thickest in its lower third, and is there slightly curved. Its weight now amounts to almost 80 grammes. These long heavy hypocotyls projecting from the fruits sway to and fro with every breath of wind. At length the vascular bundles, by which the connection with the tubular portion of the cotyledon was retained, are ruptured (see figs. 142 [7] and 142 [8]). The embryo falls away, and

its lower end bores deeply into the mud. Even a layer of water half a metre deep is pierced by it with such force that it remains standing upright in the mud beneath. After a few days the pericarp, with the cotyledon inside, is also detached. At the upper end of the fallen hypocotyl the bud which was formerly covered over by the tubular cotyledon is now to be seen. The four small green scale-leaves of this bud only increase slightly in length; but immediately, from the shoot arising from it, large elliptical shiny green leaves are developed which become active as foliage; whilst from the lower end of the hypocotyl which has bored into the mud, as well as from the epicotyl itself, roots arise which are at once the means of fixing the plant in the muddy shore, and of conducting food-salts to it. In the neighbourhood of old mangrove trees, dozens of these young plants may be seen, which have fallen and bored their way into the mud; and on the shoots produced from their upper ends sometimes only scale-leaves, and sometimes foliage-leaves are developed. The illustration opposite, taken from a sketch near Goa, on the coast of Bombay, drawn from nature by Ransonnet, shows all this very clearly.

The second form of cotyledon to be brought forward is that which occurs in grasses, and is called by botanists the *scutellum*. Although variously modified, it is in the main developed similarly in the many thousands of different species. The small embryo of the grass is in lateral contact with one end of the large starchy reserve-tissue, by means of its cotyledon, as shown in the grain of wheat chosen as type (see figs. 141 [4] and 141 [5]). The free edges of the cotyledon arch over the embryo bud, sometimes actually curling round it, forming a sheath-like envelope. Below, the cotyledon is continued into a sac which incloses the radicle of the embryo. When the materials are conveyed from the reserve-tissue to the hypocotyl, radicle, and embryo-bud, by means of the absorbent cells of the cotyledon described on p. 600, these portions quickly increase in length. The radicle pierces the sac-like envelope, penetrates into the ground, and unites by abundant root-hairs with the particles of the soil. The bud also elongates and the leaves grow up into the light from the sheath-like envelope of the cotyledon. The lower leaves are usually scale-leaves without green blades, but the leaves following these all exhibit large green laminæ which function as foliage. The starch of the reservoir is soon completely consumed in the rapid growth of the embryo. As soon as this has happened the cotyledon has no further task to fulfil, it shrivels and perishes, but the young grass-plant with its roots and its green foliage-leaves is now in a position to manufacture for itself the substances necessary for its further construction.

The third form of cotyledon is shown in the embryos of sedges and rushes, of irises, snowdrops, narcissus, aloes, and butcher's-broom, of flowering rushes, bananas, and palms, and numerous other plants belonging to the class of monocotyledons. In all these plants the embryo is embedded in the reserve-tissue of the seed, and the cotyledon proceeding from the hypocotyl forms a sheath surrounding the bud situated upon it. The cotyledon is provided with absorbent cells only at

its apex, and is connected with the cells of the reserve-tissue at that point. In germination the cotyledon increases in length and pushes the hypocotyl with the embryonic bud and radicle out of the seed. The food absorbed from the reserve-tissue by the remaining portion of the cotyledon is conducted from the interior of the seed to the extruded embryo by the lengthened part of the cotyledon. With

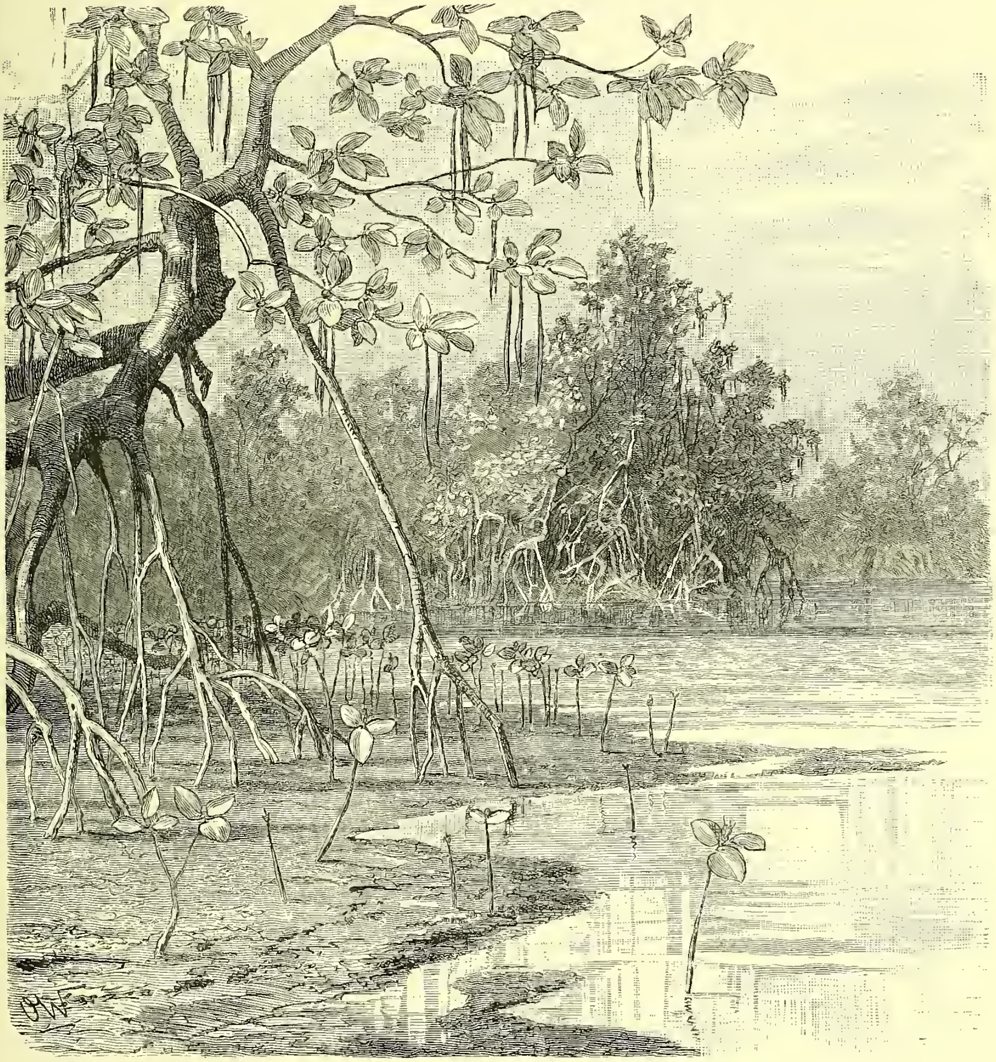

Fig. 143.—Mangroves near Goa on the West Coast of India at ebb-tide.

the help of food thus conveyed to it, the embryo is enabled to develop its radicle into an absorbent root penetrating into the ground, and also to develop its leaf-rudiments into green leaves. Numerous modifications of the process here only sketched quite generally may be distinguished, and these consist chiefly in the varying direction and length of the portions of the cotyledon thrust out from the seed. In sedges, rushes, and cyperuses germinating in marshy ground, or even

in the mud under water, the extruded portion of the cotyledon surrounding the embryonic stem, with its bud and first shoot-leaves, becomes bent upwards after it has issued from the interior of the seed (see figs. 144[14] and 144[15]), while in species of *Yucca* and *Tradescantia* it grows downward in an arch (see fig. 141[9]); and in cycads and palms, growing in soil exposed superficially to drought, it bends round immediately after its exit from the seed, and penetrates vertically into the deeper layers of earth which are always somewhat moist (see figs. 144[7, 9, 10.]). In the Areca-palm and the slender *Chamædorea* the sheath-like extruded portion of the cotyledon is very short, while in the Commelynaceæ it is much elongated, so much, indeed, that it looks as if the sheath-like portion surrounding the hypocotyl and the bud were connected by a long thread with the absorbent portion which remains behind in the seed. This central portion of the cotyledon is also much elongated in the Date palm and in the Cocoa-nut palm, as well as in the cycads *Zamia*, *Ceratozamia*, *Encephalartos.* The figs. 7, 8, 9, 10 of the illustration opposite show all the stages of development in the Date seedling. As long as the cotyledon has not pushed out from the interior of the seed, it forms a mantle-like envelope for the bud of the hypocotyl, and is continued into a sac-like covering for the radicle. At germination the cotyledon increases much in length; the free end is sheath-like, the middle portion forms a stalk-like, rolled-up structure, and the part remaining behind in the seed forms a hollow cone which becomes dilated like a vesicle where absorption of the reserve materials occurs (figs. 144[9] and 144[10]). In a still later stage the radicle develops into a root, and breaks through its sac-like covering, while the scale-leaves of the epicotyl stretch, and push their way out of the cotyledonary sheath (fig. 144[8]). Gardeners employ what they call a "dibble", a tool by the help of which the seeds and seedlings are planted in a suitable depth of earth. One is involuntarily reminded of these dibbles in observing how the tubular, rolled, stalk-like cotyledon-sheath—which grows out of the seed—not only pushes the embryo out of the interior, but presses it deeper and deeper into a layer of earth which by its depth is protected from drying up; there it is planted in a suitable place—actually in the most favourable position. In many palms the cotyledonary sheath is half a metre long, and many months pass before all the reserve-materials of the gigantic seed, often weighing as much as 8 kilograms, are conducted by this sheath to the embryo planted below.

Numerous species of Onion (*Allium*), and of Reed-mace (*Typha*) exhibit our fourth form of cotyledon. The extrusion of the embryo by the cotyledon is conducted in the same way as in the type just described, but there is this essential difference, that here the cotyledon, after it has absorbed the reserve-materials of the seed by its apex, entirely vacates the cavity of the seed-coat, becomes green, and then acts like a foliage-leaf. In the seed of the Garlic (*Allium sativum*) the embryo is embedded in the centre of the reserve (*cf.* fig. 141[17]). As soon as germination begins, the cotyledon pushes its way out of the seed-coat, and grows first upwards, then bending round at an angle, so that the extruded end surrounding the hypocotyl and the bud, comes to lie below the

level of the seed (figs. 141[18] and 141[19]). Here long root-fibres develop from the radicle and from the base of the hypocotyl; these burst through the cotyledon, grow down into deeper layers of earth, and fix the young plants in the spot where the cotyledon has placed it. The apex of the cotyledon remains in the

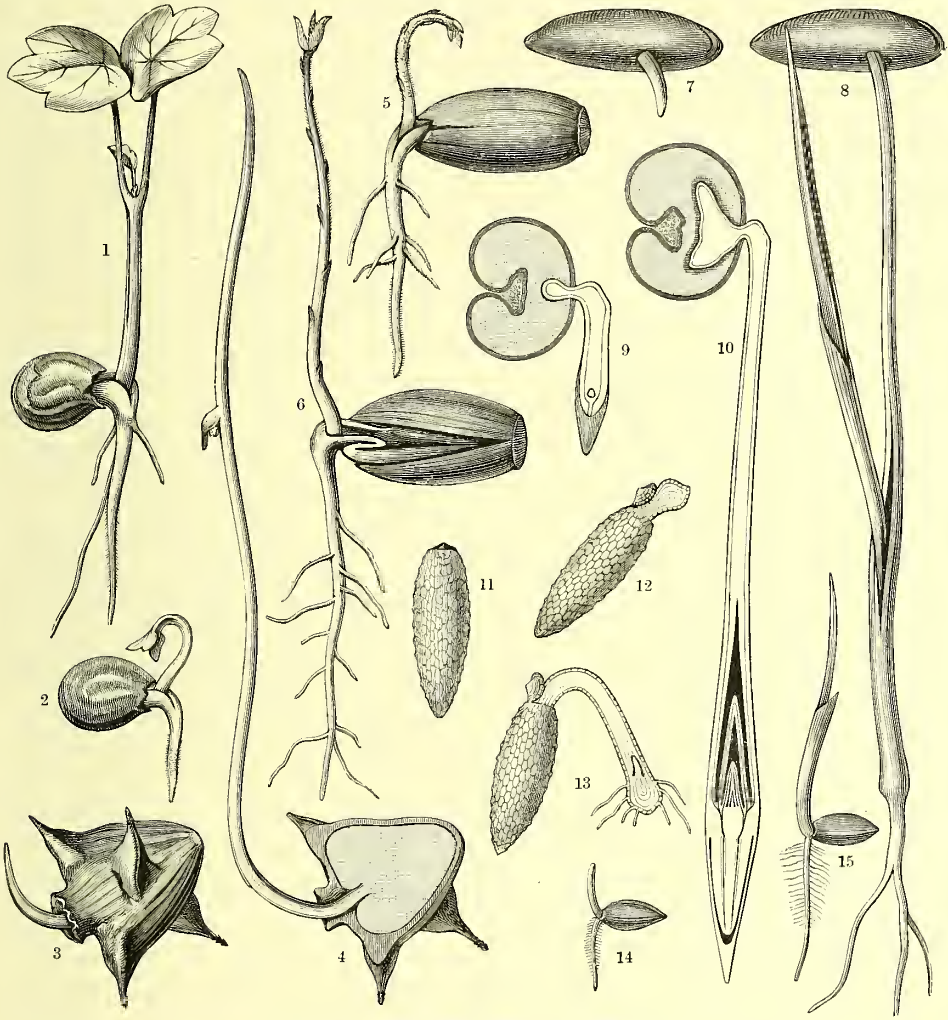

Fig. 144.—Germinating Seeds and Seedlings.

[1] Seedling of the Nasturtium (*Tropæolum majus*). [2] The same at an earlier stage of development. [3] Water Chestnut (*Trapo natans*), from which the embryo is emerging. [4] Later stage of development. [5] Young seedling of the Austrian Oak (*Quercus Austriaca*). [6] The same, further developed. [7] Seed of the Date (*Phœnix dactylifera*) from which the embryo is emerging. [8] The same eight weeks later, after the seedling has already developed root and scale-leaves. [9] Young Date in longitudinal section. [10] Older Date in longitudinal section. [11] Seed of the Reed-mace *Typha Shuttleworthii.* [12] The same with protruding embryo. [13] The same at a later stage of development. [14], [15] Seedling of the Sedge *Carex vulgaris*. Fig. 1–8, natural size; 9, 10, × 8; 11–13, × 4; 14, 15, × 6.

seed, and here absorbs the last remnants of the reserve-materials. When these are at last exhausted, one limb of the bent cotyledon grows upwards, and its apex is drawn out from the emptied seed-coat. All this occurs underground. Now the cotyledon also has to reach the sunlight and become green. This is

brought about by the knee of the upwardly-growing cotyledon acting like a wedge, and thus making a path upwards through the ground. This penetration of the ground is materially assisted by the presence of cells on the convex side of the knee which, unlike the other superficial cells of the cotyledon, are somewhat curved outwardly, and highly turgescent—a contrivance which will be described more in detail later on. When finally the free end of the cotyledon has been drawn out of the ground, the knee-shaped bend is obliterated as the green cotyledon straightens out.

The germination of the Reed-mace (*Typha*) is quite peculiar. The small fruits which are blown off the spike, fall on to the surface of the water and remain floating for some days. Then the pericarp opens and the seed sinks slowly down into the water. The husk of the seed is pointed at one end, and at the other is closed by an extremely pretty trap-door (*cf.* fig. 144[11]). While sinking through the water the pointed end is turned downwards, and the covered end upwards. At the bottom the seed lies in the position indicated and germination commences. The cotyledon grows in length, pushes open the trap-door, and makes its appearance at the mouth of the seed-coat (fig. 144[12]). It now describes an arch and the end in which are concealed the hypocotyl and the bud reaches the mud. Scarcely has it done so, however, when its epidermal cells elongate and form long tubular structures which penetrate into the slime, and the free end of the cotyledon is thus firmly fixed (fig. 144[13]). Later on rootlets make their appearance, which, proceeding from the hypocotyl, break through the unresisting cotyledon. Meanwhile the reserve food has been sucked up by the apex of the cotyledon which remained in the seed; this apex is now drawn out of the seed-coat, the cotyledon straightens itself, turns green, and functions as a foliage-leaf.

In the four cases just described the embryo only possesses one cotyledon, and each seed contains a reserve-tissue beside the embryo. In the fifth case now to be described, however, the embryo is equipped with two cotyledons, and the building materials which are at its disposal for the first period of growth are stored up in the embryo itself, almost entirely indeed in the cotyledons. To this class belong plants with stone-fruits as well as most species with seeds and fruits of nut-like appearance, and many the seeds of which have a softer, leathery covering. As examples may be named the Walnut and Hazel, the Oak, Chestnut and Horse-chestnut, the Almond, Cherry, Apricot, and Peach, the Laurel and Pistachio-nut; the Nasturtium (*Tropæolum*), Broad-bean, the Scammony (*Cynanchum*), and the Bastard-Balm (*Melittis*). The two leaves proceeding from the hypocotyl almost completely fill the space inclosed by the seed-coats in all these plants; and the small embryonic bud as well as the radicle are situated between the two cotyledons, just like a dried plant between the sheets of paper in a herbarium. The cotyledons are thick, swollen, and tense, of fleshy appearance in section, and always comparatively heavy. Many of them are wavy, and they rarely look leaf-like. Occasionally the two cotyledons are fused together

by their adjacent surfaces, as, for example, in the Chestnut, Horse-chestnut, and Nasturtiums. Everything which one is generally accustomed to consider an attribute of a leaf is entirely wanting. When these seeds take up water from the environment and begin to germinate and grow, first of all the seed-coat bursts at one end of the seed, and the radicle together with the axis and also the thick stalks of the two cotyledons are extruded through the rupture. The cotyledons themselves, however, remain inside, lose weight in proportion as they give up materials to the growing parts, dwindle, and finally appear quite shrivelled and emptied. The extruded radicle has, on the contrary, visibly increased, it bends downwards, penetrates vertically into the ground, and produces lateral roots with root-hairs, which now absorb nourishment from the soil. The bud which was hemmed in between the short thick stalks of the two cotyledons has, on the other hand, curved upwards, elongated pretty quickly, and become a shoot which in the Nasturtium immediately develops green, lobed foliage-leaves. In other plants, *e.g.* in the Oak, first scale-leaves appear and then green foliage-leaves above them. In fig. 144 [1, 2, 5, 6] these conditions are depicted both in the Nasturtium and the Oak. The cotyledons have here a threefold part to play; first of all they function as storehouses for reserve materials, and at the same time as protecting envelopes for the small squeezed rudiment of the future plant; in addition they also have the task of thrusting the embryo out of the cavity of the seed so far that its members can elongate as required—some towards the light, and some into the dark ground. When they have performed these duties they die off and disintegrate so completely that at the place where they were connected with the hypocotyl, scarcely a trace of their insertion is to be recognized.

A peculiar condition of the cotyledons, the sixth in the series here described, is observed in the Water Chestnut (*Trapa*). One of the cotyledons is small and scale-like, containing no reserve materials; the other is very large, and so completely fills up the nut that it looks as if someone had poured wax into the interior of the fruit, and that it had there become hardened into a solid mass. The Water Chestnut germinates on the mud under water. As soon as germination commences, a white worm-like body is extruded from the aperture of the nut, and though many consider this to be the hypocotyl, it should, strictly speaking, be regarded as a root (*cf.* fig. 144 [3]). This structure elongates under the water and grows directly upwards. Of the two cotyledons only that one which was inserted as a tiny scale on the short hypocotyl, leaves the cavity of the nut and is connected by a long stalk with the hypocotyl. This long stalk, together with the very small hypocotyl and the root, pass so gradually into one another that they resemble a single unjointed white cord (*cf.* fig. 144 [4]). The reserve materials deposited in the large, fleshy cotyledon are conducted by the stalk-like connection to the growing parts of the embryo in the water; a process which occupies a considerable time. By the time that this cotyledon has yielded up the reserve food, the root has grown so strong that it is able to take up materials from its surroundings; it bends down towards the mud

in which it fixes itself by numerous lateral fibres. The bud has meanwhile grown out and formed a shoot which develops scale-leaves below, with green foliage-leaves above these, and so grows up to the surface of the water. The exhausted cotyledon never leaves the interior of the nut, but gradually decays with it. Thus we have here the rare instance of one cotyledon being extruded from the cavity of the seed (that is to say, of the fruit) while the other remains behind.

In the seventh case the embryo exhibits two (only exceptionally more than two) cotyledons, which are drawn out of the seed-coat during germination, and spreading out in the sunlight, turn green and serve as foliage-leaves. These foliage-leaves first function as absorbent organs; that is to say, they adjoin a special reserve-tissue in the seed from which they derive the materials required for their first growth, and do not issue from the cavity of the seed until the storehouse is exhausted and emptied of food. This is the case, for example, in the repeatedly-mentioned Corn-cockle (*Agrostemma Githago*), whose two cotyledons, folded together, are bent like a horse-shoe round the reserve-tissue, but are withdrawn from the seed-coat after the consumption of this food, when they separate and become green (*cf.* 141 [7, 8, 9, 10]). Much more rarely the seed-coat bursts at the beginning of germination, the large folded cotyledons together with the surrounding reserve-tissue are drawn out so that the absorption of the reserve-food does not take place till after vacating the seed-coat, after which follows the unfolding and colouring of the two cotyledons in the sunlight. The seeds of *Ricinus* (*cf.* figs. 141 [1] and 141 [2]) show this process of development, which on the whole is very uncommon. On the other hand, it frequently happens that no special reserve-tissue (endosperm) is present, that the small amount of reserve-food is deposited in the cotyledons themselves, and that immediately after germination has commenced the two cotyledons leave the cavity of the seed-coat and become green foliage-leaves. As an example of this the germination of the Gourd (*Cucurbita Pepo*) is given in fig. 145 [1].

The way in which cotyledons are withdrawn from the cavity of the seed-coat is very characteristic, and it is worth while to inspect the most remarkable contrivances of this kind somewhat more carefully. One of the most peculiar is observed in the seed and embryo of the Gourd, which is figured opposite in natural size. The seed of the Gourd is pretty large, flattened, oval in outline, rounded at one end, and somewhat tapering at the other, and here cut off short, and provided with a small aperture. If these seeds are disseminated they lie flat on the ground, and easily glue themselves to the soil, especially if their surface is covered with the adhesive juice of the fleshy fruit, as is always the case when the seeds are naturally distributed. Since the embryo inclosed by the seed-coat is straight, it has a position parallel to the surface of the ground. When germination begins the radicle is first of all pressed out through the small opening mentioned. It immediately arches and grows quickly downwards into the earth by the help of the food conveyed to it by the two cotyledons. It there develops lateral rootlets, and unites firmly with the

particles of soil by means of abundant root-hairs. The hypocotyl also, into which the root merges, grows at first downwards into the earth, but of course only for a short time, for this is very soon altered; and growth then takes place in an opposite direction towards the light, and immediately after this alteration of direction the withdrawal of the cotyledons commences. It follows from what has been said that the hypocotyl is fixed both above and below—below by the root which has grown

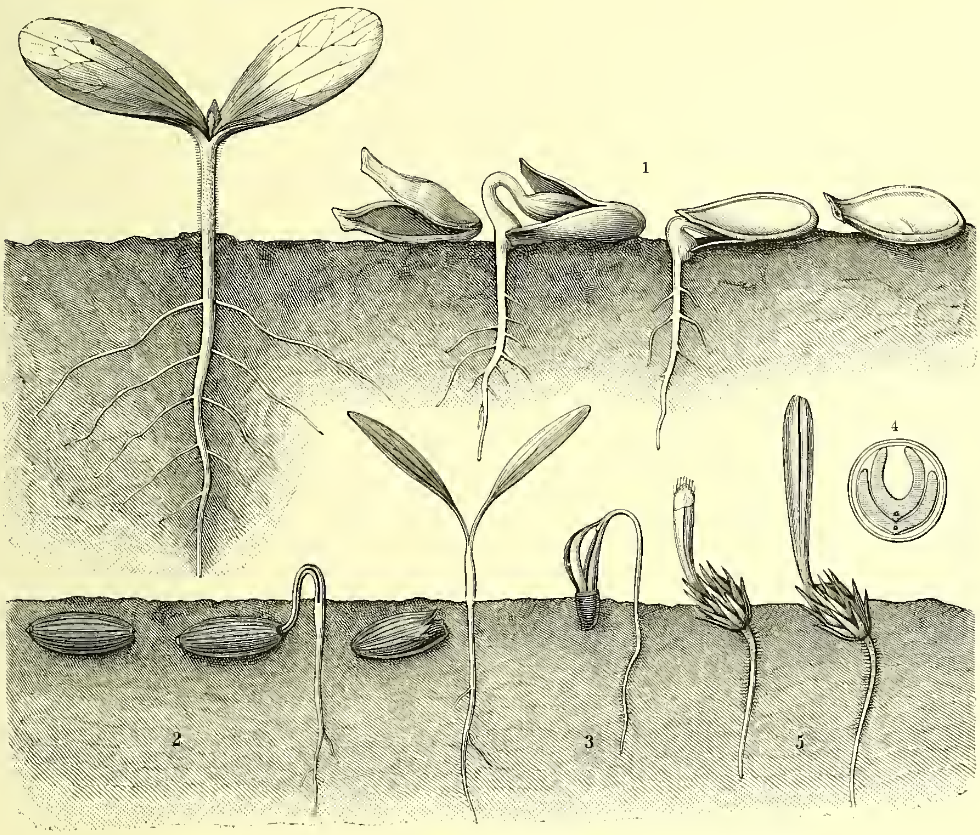

Fig. 145.—Liberation of the Cotyledons from the cavity of the seed or fruit husk.

[1] Gourd (*Cucurbita Pepo*). [2] Asafœtida (*Scorodosma Asa fœtida*). [3] Immortelle (*Helichrysum annuum*). [4] Cross-section through the cotyledons, showing them curled up in the pericarp of the Immortelle. [5] *Cardopatium corymbosum* (after *Klebs*). Fig. 1-3, natural size; fig. 4-5, somewhat enlarged.

firmly into the ground, above by the firmly glued seed-covering in which the cotyledons lie. As soon as it increases in length it forms a well-marked arch, frequently even a loop, with the convex side turned upwards (*cf.* fig. 145 [1]). Naturally it thus exercises a severe strain on both ends. The root, well planted in the earth, can no longer be disturbed from its position, but the effects of the tension make themselves felt on the cotyledons, which still lie in the seed. The coat of the Gourd seed bursts, the cotyledons are drawn out from the yawning cleft, the hypocotyl straightens itself, and the two cotyledons separating from each other turn their upper sides towards the light (fig. 145 [1], on the left).

The splitting of the seed-coat and the withdrawal of the cotyledons in the Gourd are materially assisted by the development of a projecting lip at the union of the radicle and hypocotyl. This lip presses against the lower edge of the hard seed-coat, and holds it to the ground, so that after the bursting takes place the upper portion of the seed-coat is raised up lid-wise from the lower. A smaller projection is also developed on the hypocotyl in the embryo of the Sensitive Plant (*Mimosa pudica*), and in that of *Cuphea*, and here again it presses against the lower part of the seed-husk, and so assists both the bursting and the withdrawal. When the seeds are surrounded by a pericarp, sometimes bands and projecting corners are developed on it, sometimes projecting edges of the dried calyx and the like, which serve as a fulcrum to the lip of the hypocotyl. The presence of numerous structures formerly considered to be stunted organs useless to the plant thus receives its natural explanation.

Many plants, *e.g.* certain Umbelliferæ, develop a very short hypocotyl. This does not bend, and exercises only an insignificant strain, or perhaps none at all, on the cotyledons, and so would not be able to release them from the integument of the seed or fruit-husk. In all these plants the cotyledons have long stalks, and these assume the function of the hypocotyl, at least in so far as the withdrawal of the blades of the cotyledons is caused by them in the same way. This phenomenon is very noticeable in the germination of the Asafœtida (*Scorodosma Asa fœtida*), as is clearly shown in fig. 145 [2]. The stalks of the cotyledons, arising from the very short hypocotyl, rapidly elongate, and exhibit the same S-shaped bend as that formed in the hypocotyl of the Gourd seedling. These stalks also produce a similar effect on the blades of the cotyledons still lying within the fruit-husk, and actually draw them out. As soon as this has happened, the stalks straighten, and the blades borne by them turn their upper surfaces towards the light.

Almost a third of all seed-bearing plants have cotyledons whose liberation from the bondage of the seed-coat or pericarp is effected in this manner, and this consequently is the form of cotyledons which has been most frequently observed and described. Much less frequently the two cotyledons make their appearance at one end of the pericarp or seed-coat, while the radicle grows out at the opposite end. In this case, which must be regarded as the eighth of the series here given, the embryo is straight, and the hypocotyl is short and bears two thick cotyledons whose apices, lying close together, form a truncated cone. When the radicle has been once pushed out, and has planted itself firmly in the ground, the hypocotyl at once elongates in the opposite direction without bending, pushes the folded cotyledons in front of it, and presses them out of the fruit-husk. The tissue of the fruit-husk lying above the cotyledonary cone must be pierced, and this is not difficult to do, since this tissue consists of thin-walled cells. When the radicle has grown out from one pole, and the pair of cotyledons from the other, the seedling is surrounded half-way up by the vacated fruit-husk, as though by a girdle (*cf.* fig. 145 [5]). The apices of the cotyledons still folded cone-like together usually bore through the soil above the husk after they have left the cavity, and

not until this has occurred do they unfold and become green. In this penetration of the earth the cotyledons are exposed to so many dangers that special arrangements are frequently to be found with a view to protecting their advancing points.

As the cotyledons push through the ground, a pressure is exercised upon the layers of soil above by the straightening of their stalks. The cotyledons raise portions of soil on their backs, so to speak, without actually bursting or boring through them. In this way the danger of injury is at any rate much diminished, and the supposition is fully justified that cotyledons which develop after the type of the Gourd or Asafœtida are those which occur most frequently. Plants whose straight embryo has to pierce through the fruit-husk and the layer of earth above it by means of their conically-folded cotyledon apices are, as already stated, less common. Fig. 145 [5] shows this rare form in *Cardopatium corymbosum.* It has also been observed in many other species allied to this composite, and in the Mediterranean *Atractylis cancellata.*

In all those cases where the cotyledons are withdrawn through a cleft or hole in the seed-coat it seems quite obvious that the aperture should have a diameter at least equal to that of the organs to be withdrawn. As a rule this is so; but occasionally the cotyledons are actually broader than the cleft, and one asks in astonishment how the withdrawal could have been accomplished without injury to their fabric. The feat is performed in the following way. Before the strain on the cotyledons comes, they are folded together, and are then drawn out as a long roll through the narrow opening of the integument. Scarcely have they been liberated ere they begin to unroll and spread themselves out flat. This is the case, for example, in the Immortelle (*Helichrysum annuum*) (see figs. 145 [3] and 145 [4]), also in the umbellifer, *Smyrnium Olusatrum,* and in many others. In some plants, *e.g.* in the Beech (*Fagus sylvatica*), the cotyledons, as long as they remain within the husk, are folded together lengthwise like a fan, and in this position occupy but a limited space. They are also withdrawn from the nut through a comparatively small aperture, and then expand in a very short time after they are free (see figs. 148 [1, 2, 3]). The two cotyledons of *Pterocarya caucasica* are each divided into four lobes, and each pair of lobes lying close to one another are imbedded in a special excavation in the seed. Altogether the fruit presents four compartments, in each one of which lies such a pair of narrow, closely-packed lobes. The aperture of the nut-like pericarp now affords sufficient space for each pair of folded lobes to be drawn out, nor does their withdrawal occur simultaneously, but rather so that the pairs of lobes emerge one after the other. The cotyledons of *Schizopetalon Walkeri* behave in a similar manner, each of them being divided into two long narrow lobes which are drawn out successively through the small aperture of the spherical seed. Moreover, in the embryos of *Pinus* there are five or more whorled linear cotyledons (see fig. 148 [6]). These also leave the cavity of the seed one after the other. Speaking generally, it would seem that the dimensions and form of the cotyledons are correlated with the shape of the seed-coat or other investment, and with its manner of opening.

The external form of the seed and the position which it consequently assumes on falling to the ground is by no means an unimportant item in this connection. If the seed comes to lie so that the axis of the hypocotyl is perpendicular to the surface and the tip of the radicle is directed downwards, we seem at first sight to have a very favourable position for germination; but it is not so in reality. In this position the hypocotyl would have to perform the most complicated curves in order to be able to withdraw the cotyledons from the seed. On the other hand, the most favourable condition is obtained when the axis of the hypocotyl and radicle lie parallel to the surface of the ground, as, for example, in the gourd seeds illustrated in fig. 145 [1]. Here the radicle immediately after leaving the seed-coat can bend down at a right angle and grow into the earth, and the hypocotyl is able to withdraw the cotyledons very rapidly. When seeds of this sort are sown, they usually assume the last-mentioned position. Flat or compressed seeds lie with their broad surface on the ground; oval and elongated cylindrical seeds fall so that their longer axis is parallel to the substratum; whilst in spherical seeds the centre of gravity is so situated that the most favourable position possible for germination is obtained.

The importance of numerous developments on the exterior of the seed-coat or pericarp will at once become evident to anyone who observes attentively the process of withdrawal of cotyledons. It is manifest that the withdrawal only occurs without delay when the seed is in some way or other firmly fixed and when arrangements are present which prevent a favourable position being lost when once assumed. This would not be so were the seed the plaything of every gust of wind or current of water. Equipments for retaining fruits and seeds in the position of germination occur in great number and variety. Even the wing-like and hairy appendages, the curved, pointed, and barbed processes, and the various adhesive arrangements of fruits and seeds, which in the first instance have the function of agents for distributing the fruits, often afford this advantage, viz. that by their means the seeds are fixed where germination can successfully take place. If we look at the damp mud by a river's bank, towards the end of May, when the fluffy seeds of willows and poplars are escaping from the dehisced fruit-capsules and are carried along by the wind, we there see countless numbers of these seeds sticking by their hairs to the mud so tightly that they cannot readily be displaced. All such seeds (differing from the generality of seeds) germinate in a few days, while seed lying on the ground in loose flakes close by do not germinate. The hairy coat which first served as an agent for distributing the seed, now functions as an agent for fixing it in the germinating bed. This also applies to the tufts of silk adorning the small seeds of tropical tillandsias (*Tillandsia usneoides* and *T. recurva*) which grow as epiphytes on the bark of trees. These first serve as wings, and the tiny seeds are carried by the wind far away from the burst fruit-capsules. If these seeds are stranded on the bark of a tree-trunk which is swept by the wind, the hairs cling firmly and bring the seeds

into contact with the substratum. Accordingly the weather side of the trunk is seen to be beset with large numbers of such seeds, and many of them, pressed into the crannies of the substratum, begin to germinate. A similar process is observed in the settling of the seeds of *Anemone sylvestris* and many composites. To cite yet another example, we may name the hooked fruits of *Xanthium spinosum* and *Lappago racemosa.* When detached from their place of origin by wandering animals, these seeds remain fixed by their barbed processes to the hairy coats of the animals, and thus are often removed considerable distances. Naturally the animals try to free themselves from these irritating appendages by rubbing themselves against the ground until they detach the fruits from their coats. In this way a part of the fruits are pressed into the soil, and are there anchored by their barbed spines. Only the embryos of the firmly-anchored fruits develop into vigorous plants; those seeds which lie more loosely on the ground, on the contrary, either do not germinate at all, or the seedlings whose cotyledons are imperfectly withdrawn from the pericarp soon perish.

Besides these outgrowths, which, as we see, possess a double function, there are also those which have no connection whatever with distribution, and have apparently no other use than to fasten the seeds to the germinating bed. In this connection we have first to notice adhesive materials which exude from the surface of the seed-husk, whereby the seeds are cemented to the soil. These make their appearance when the surface of the seed is moistened, as when water is sucked up by the seed from the soil of the germinating bed. Usually the slimy cement arises from the superficial cells, as, for example, in the many species of flax and plantain (*Linum* and *Plantago*), in the Cress and the Gold-of-pleasure (*Lepidium sativum* and *Camelina sativa*), in *Teesdalia, Gilea,* and *Collomia,* and in many other species of the most diverse genera. All, however, agree in this particular, that the seed-coat possesses a smooth, polished surface. In the Basil (*Ocymum Basilicum*) and in the numerous species of *Salvia* and *Dracocephalum,* the mucilaginous substance arises from the smooth surface of the pericarp. Frequently the adhesive mucilage is only developed in certain cells arranged in rows on the surface of the fruit or seed-husk, as in the New Zealand *Selliera* and in numerous Compositæ, of which the Wild Chamomile (*Matricaria chamomilla*) may be cited as the best-known example. In *Oxybaphus* there are five longitudinal ridges on the integument of the seed covered with small mucilage-organs. When the integument is moistened, five white slimy lines appear on it, and these bring about its adhesion to the germinating bed. In many Compositæ, *e.g.* in the common Groundsel (*Senecio vulgaris*) and in *Euriops, Doria, Trichocline,* and in many other genera, special hairs are developed on the fruit-husk which excrete adhesive mucilage. In other instances, again, as in many aroids, the cement is not developed by superficial cells, but a part of the fleshy pericarp, in which the seeds were inclosed, remains as a dried-up crust. If these seeds be subsequently moistened, the

crust again becomes changed into a mucilaginous adhesive mass which glues them to the substratum. The whole succulent decaying pericarp often becomes the fixing agent of the seeds, as, for example, in gourd-like plants, and in many plants with berries and stone-fruits.

In numerous plants, *e.g.* in the Corn-cockle (*cf.* figs. 141 [7, 8, 9, 10]), and in *Neslia paniculata* which grow abundantly in loamy fields, the fixing of the fruits or seeds to the soil is not effected by mucilaginous cement-materials, but by inequalities on the surface of the integument. Here are developed extremely diversified warts, pegs, ridges, or net-works, and between them pit-like depressions into which the earth-particles penetrate, and when moistened become closely connected with the superficial cells. The adhesion is therefore very close, and if we try to cleanse these seeds or fruits, and to remove the clinging soil from all the small hollows, we shall not completely succeed even after a great deal of trouble. And here we must point out the interesting distinction between rugged seeds like these, and such as become slimy. Seeds with rough, wrinkled, and pitted surfaces never develop adhesive agents, since they are fixed to the soil by these inequalities of the seed-coat; on the other hand, seeds with smooth surface, which would otherwise be easily displaced, adhere by means of mucilage developed by their epidermal cells.

The Water-chestnut (*Trapa*), whose germination was described on p. 609, behaves in a very peculiar manner. Each of its large fruits exhibits two pairs of projecting spines arranged cross-wise, which have been formed from the sepals, and which protect it during ripening from the attacks of aquatic animals. These spines, as well as the whole fruit, are as hard as stone, but only in the interior. The outer cell-layers are soft, decompose quickly under water, and separate from the deeper tissue in irregular tatters and shreds. At the apex of the spines, after the detachment of the soft portion there remain not only the strong hard midrib, but also the commencements of some recurrent bundles of very firm elongated cells which spring from the midrib immediately behind the apex. These spines therefore have the appearance of anchors (see fig. 146), and indeed they function as anchors, adhering at the bottom of the lake by means of their barbed points to various vegetable remains which cover the mud, and are actually anchored there. The seedling arising from the nut does not consequently lift the pericarp with it, but this remains fixed in the place where it fell.

Peculiar contrivances for anchoring fruits to spots suited for germination are observed in many steppe-grasses, especially in the Feather-grass (*Stipa*) and in the Stork's-bill genus (*Erodium*). The feather-grasses are a striking feature of steppes; indeed, together with various Papilionaceæ—especially with tragacanth shrubs (*Astragalus*)—and with numerous Compositæ, pinks, and low irises, they compose the chief constituent of the vegetation. Ernst Heyn, in the accompanying Plate VI., "Feather-grasses on a Russian Steppe", has shown such a steppe and its characteristic vegetation with complete fidelity to nature. To this picture

1. *Stipa pennata.*
2. *Ranunculus pedatus.*
3. *Astragalus exscapus.*
4. *Astragalus virgatus.*
5. *Dianthus polymorphus.*
6. *Jurinea mollis.*
7. *Achillea ochroleuca.*
8. *Iris variegata.*
9. *Astragalus Onobrychis.*
10. *Salvia Austriaca.*
11. *Syrenia angustifolia.*
12. *Festuca vaginata.*

PLATE VI.

FEATHER GRASS ON A RUSSIAN STEPPE.

Printed from the originals by the BIBLIOGRAPHISCHES INSTITUT, Leipzig.

we shall have repeated occasion to refer. The Feather-grass at once claims our attention in the drawing by its tufts of white feathery streamers swinging in the wind. These structures are awns, which have elongated in this remarkable manner since the time of flowering of the grass.

The glume, which is crowned with the feather-like awn, together with a second short glume, destitute of awn, incloses the small fruit. As soon as it is ripe, the fruit, wrapped in its glumes, becomes detached; the first breeze carries it off and blows it like down over the steppe. The long feathery awn arising from the glume has thus, in the first instance, the significance of a flying apparatus, like so many of the feathery or wing-shaped structures which beset or envelop seeds and fruits. It effects the distribution of the feather-grass in question over wide

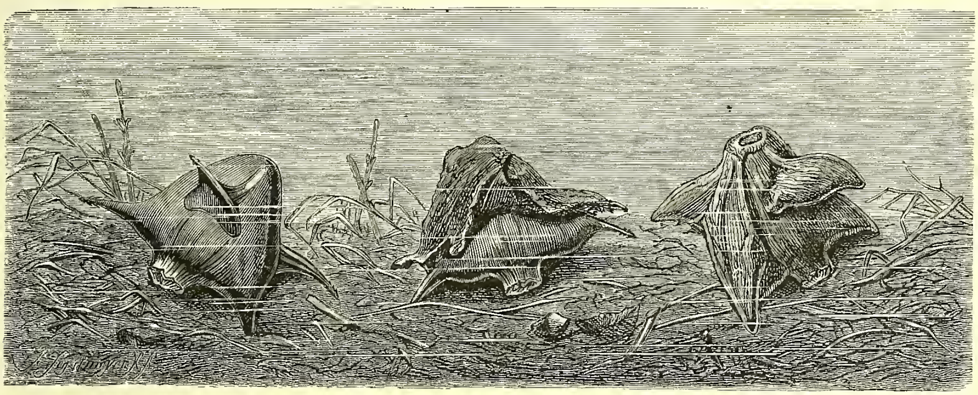

Fig. 146.—Anchoring of the Water-chestnut (*Trapa*).

tracts of country. But after the awn has become stranded somewhere on the soil of the steppes, it has yet another function to perform.

Let us suppose that a feather-grass fruit has fallen on to the bare earth, as in the illustration on p. 619; that part containing the fruit inclosed in the glume, as it is the heaviest, will obviously come first into contact with the ground; and since the tip of this portion is hard and sharply pointed, the stranded fruit often sticks in the ground immediately upon alighting (fig. 147 [1]). Should it fall obliquely, the tip will penetrate into the ground by the continued twisting of the long feather waving in the air. This first penetration is materially favoured by the fact that the point is bent a little obliquely towards one side.

When once the point has penetrated into the soil, the other portions of the glume surrounding the fruit soon follow, owing to the action of the following contrivance. Close above the point of the enveloping glume are inserted upwardly-directed hairs which are at once elastic, flexible, and yet stiff. As long as these stiff hairs lie close they offer no resistance to the penetration of the glume into the soil, and some of them are actually embedded in the soil even at the first penetration of the point. Now if the fruit as it pierces the ground be inclined to one side, by some pressure operating ever so lightly from above, then the hairs on that side are pressed still more closely against the glume, while those

on the other are made to stand off somewhat; these latter press against the particles of earth above them, and act as levers, by means of which the whole fruit at the moment of bending in the given direction becomes pressed down deeper into the ground. This action is continued every time the fruit wobbles from side to side, so that bit by bit it is buried. The only question is, how these sudden alterations in position of the fruit fixed in the ground can be brought about. A glance at fig. 147 shows that every wind, even though slight, which strikes the long feathery portion of the awn, must immediately be followed by an alteration in the position of the fruit. Just as a weather-cock on the top of a roof in a strong east wind does not point invariably towards the east, but generally makes short veerings to the north and south, so the plumed awns fluttering to and fro in the east wind swerve momentarily towards the north and south, and this change of direction causes the fruit sticking in the soil to incline to various sides. When the wind veers round of course an alteration occurs in the direction of the feathery awn, and consequently a more strongly-marked inclination of the fruit occurs, so that a see-sawing motion of the latter will be unavoidable. The wind, therefore, is an important factor in driving the fruit into the ground. The awns of the Feather-grass, however, have two other peculiar contrivances, viz., below the feathery portion they are bent twice like a knee, and they are also spirally twisted like a corkscrew. This bent and twisted part of the awn is exceedingly hygroscopic; in rainy weather the knee-shaped bend almost entirely disappears; the awn bristles and straightens itself, the spiral unwinds in damp weather, and twists up again in dry air. These movements are evidently conveyed to the glume, and produce alterations in its inclination, which again cause an advancement of the tip into deeper layers of earth.

These movements of the lower portion of the awn produced by the varying humidity of the air make themselves specially felt when the upper portion has in some way become entangled with the stems and leaves of the other steppe-plants, as frequently happens. When in dry weather the fruits of the Feather-grass become detached and are blown by the wind over the steppes, it is almost unavoidable that they should remain fastened by their knee-like bent portion to haulms, stems, and the like—that the feathery part should be hemmed in between two neighbouring stems of other plants, or occasionally even entangled with them (*cf.* fig. 147 [2]).

But as soon as the upper portion of the awn is fixed, and later on in damp weather the lower knee-shaped portion of the same awn has become straightened and the spiral twists uncoiled, the fruit is necessarily forced into the ground with a twisting movement, and is also pressed now to this side and now to that by the unequal straightening of the knee-shaped bend. Any backward movement of the fruit from a subsequent drying up of the awn is prevented by the above-named stiff hairs, in the manner already described. It is much more likely that one of the stems to which the awn has attached itself should be somewhat bent by this contraction of the awn, than that the glume already driven a certain depth into the ground and there anchored should be drawn out.

The fruits of the Stork's-bill (*Erodium*) get planted in the same way as those of the Feather-grass. The five mericarps (or fruit segments) in this plant detach themselves in a very characteristic manner from their support, as may be seen in fig. 147 [3]. First the lower thick end inclosing the seed splits off, and later

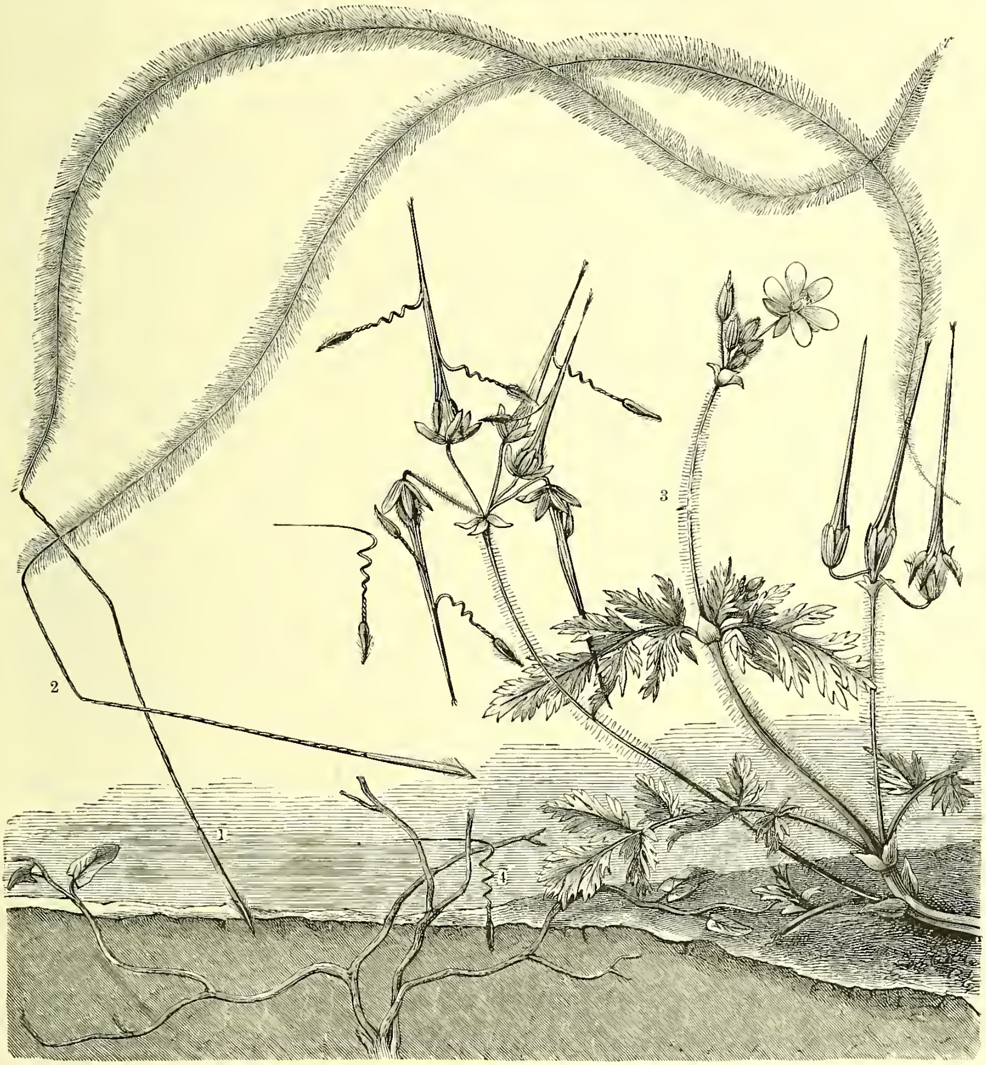

Fig. 147.—Showing the boring of fruits into the ground.

[1], [2] Fruits of the Feather-grass (*Stipa pennata*). [3], [4] Fruits of the Stork's-bill (*Erodium Cicutarium*).

also the long drawn-out point of the carpel. A part of the latter twists up spirally, and only its free end stretches out in a slight curve, like the hand of a watch. It is well known that this fallen fruit-segment is used as a hygrometer. It is placed with its lower thick end which, like the fruit-end of the Feather-grass, possesses a sharp point, on a board covered with paper, in the centre of a circle. Marks are made on the circumference of the circle corresponding to the position

of the pointer-like end of the Stork's-bill fruit in very damp and in very dry weather respectively, and we can then draw conclusions from the position of the pointer as to the relative dampness of the air. In this application of the fruit we have an exhibition of the torsions which take place in the course of its penetration into the ground, and which are produced by the alterations in the humidity of the air. When such a fruit falls on the ground, however, it is not the lower thick end inclosing the seed which is fixed, as in the hygrometer, but the pointer-like process, and consequently in nature it is the seed-end and not the pointer which is set in motion by an alteration of humidity in the air. The fixing of the fruit in the ground is naturally effected thus: the point of the arm lies on the soil, and in consequence of the untwisting of the spirals in damp weather, the thicker seed-containing end (which is provided with a sharp point) bores deeply into the ground. More frequently the fallen fruits hang between the entangled stems, &c., of other plants lying on the ground, as shown in fig. 147[4]. Here again the arm is fixed, and the thicker, lower end is set in motion. The movement may be compared to that of an augur, although in consequence of the swaying and alteration in position of the beak, unavoidable in windy weather, see-sawing movements occur in the boring part, and these are apparently advantageous. Like the fruits of the Feather-grass those of the Stork's-bill are beset above the sharp point with erect, stiff hairs. These hairs also play the same part as in the Feather-grass. According to the species various divergencies are found in the fruits of Feather-grasses and Stork's-bills. The twisting of the lowest portion of the awn generally differs from that of the knee-like bent part; the bristles on the glumes are sometimes arranged in two longitudinal rows and sometimes they form a ring below and are continued upwards as a one-sided longitudinal stripe, and so forth. Many species of *Stipa* have no plume to the awn, and approximate closely in form to the fruit of the Stork's-bill. The same remark applies to fruits of the genera *Aristida* and *Heteropogon*, which are allied to *Stipa*. But in the main all these developments agree with one another. The aim and object of the wonderful mechanism just described is not so much the penetration of the pericarp or seed-husk to a great depth into the soil, as the fixing of it firmly in the germinating bed.

It still remains to be pointed out that the cotyledons are only withdrawn without delay from their investments when the latter are firmly cemented, anchored, or fixed in some way to the substratum. When this is not the case, it often happens that the fruit, or seed-coat, is raised up like a cap by the enlarging cotyledons. The pull, otherwise exerted by the elongating hypocotyl, cannot under these circumstances assist the cotyledons in their liberation. Often, indeed, the cotyledons throw off the seed-coat unaided, but this is not always the case. In many instances their apices remain squeezed up in the cavity of the husk, stunted and yellow, and this reacts injuriously on the seedling, often causing weakness and even death. It is therefore a mistake for gardeners to plant seeds in loose earth where no good hold is afforded, since then, on germination, the seed-coats are raised up by the only half-liberated cotyledons, whose apices are still imprisoned.

With regard to the forms assumed by the cotyledons now withdrawn from the seed under favourable conditions, and which have become green in the sunlight, it is to be noticed that they present far fewer variations than those of ordinary foliage-leaves. Usually their margins are entire, their form elliptical or linear, more rarely circular and obovate. Sometimes the cotyledons are indented in front, resembling a heart in outline; this is especially the case where the embryo is folded

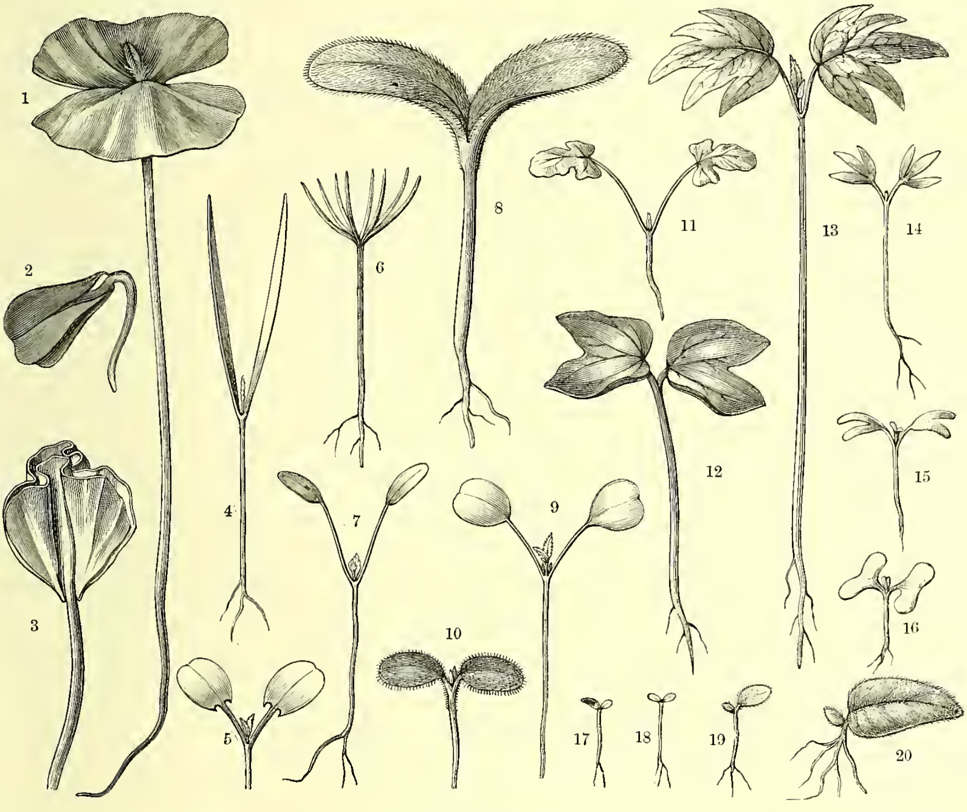

Fig. 148.—Cotyledons.

1, 2, 3 *Fagus sylvatica.* 4 *Fumaria officinalis.* 5 *Galeopsis pubescens.* 6 *Abies orientalis.* 7 *Convolvulus arvensis.* 8 *Borago officinalis.* 9 *Senecio erucifolius.* 10 *Rosa canina.* 11 *Erodium Cicutarium.* 12 *Quamoclit coccinea.* 13 *Tilia grandifolia.* 14 *Lepidium sativum.* 15 *Eucalyptus orientalis.* 16 *Eucalyptus coriaceus.* 17–20 *Streptocarpus Rexii.*

in the seed, so that the radicle lies close to the outer margin of the cotyledons, and may be explained as an economy of the scanty space within the seed. Most rarely of all the cotyledons are two-lobed (*Raphanus sativus*), and bisected (*Eucalyptus orientalis, Eschscholtzia Californica*), three-lobed (*Erodium Cicutarium*), and trisected (*Lepidium sativum*), four-lobed (*Pterocarya Caucasica*), and five-lobed (*Tilia*). It is still to be mentioned that in all seedlings whose hypocotyl is short, the blade of the cotyledons has a long stalk, while in seedlings with elongated hypocotyls the blade is sessile. This is connected with the processes already mentioned, and also partly with the fact that it is of importance to seedlings that

their green blades should be exposed as much as possible to the sun, and that so they should rise above other objects which might place them in the shade. The accompanying figure 148 shows the most noticeable forms of cotyledons after they have unfolded and spread out in the sunlight.

When two green cotyledons are present they are usually similar in shape and size, only that which has served in the seed as an absorbent organ is generally somewhat smaller in the adult condition, as, for example, in the Corn-cockle, Mustard, and Hemp. Frequently the limited character of the space within the seed makes it necessary that one of the cotyledons should give place to the radicle, or that it should only attain to an inconsiderable development, as, for example, in *Petiveria* and *Abronia*. In species of *Streptocarpus* belonging to the Gesneraceæ (see figs. 148 [17, 18, 19, 20.]), the two cotyledons have the same shape and size in the seed, after they have left the seed-coat they are still entirely similar, but later on the growth of one is retarded, and it dies, while the other increases to an extraordinary degree, and develops into a green foliage-leaf lying on the ground, 22 cm. long, and 12 cm. broad. Strangely enough, many species of this genus, *e.g.* *Streptocarpus polyanthus* develop no other green leaves, but content themselves with the development of the one cotyledon into a gigantic foliage-leaf prostrate on the soil, with which later on the epicotyl appears to be united, and from whose thick midrib it rises up as a flowering axis.

It is without question that cotyledons which become green possess, in common with other green tissues, the property of manufacturing organic materials in the sunlight from the absorbed food-gases, salts, and water. As a rule chlorophyll does not appear until the cotyledons have issued from the seed-coat, and have spread out in the sunlight. It is, however, sometimes formed even while the cotyledons are still in the seed and shrouded in darkness, as, for example, in firs and pines, in maples, and some Cruciferæ, in Loranthus, Mistletoe, and the Japanese Sophora. Green cotyledons exhibit all the characteristics of foliage; their epidermis is provided with stomata, whilst palisade-cells and spongy parenchyma can usually be distinguished in the green tissue. Many plants, especially those which subsequently develop subterranean tubers, or tuberous roots, *e.g.* many species of *Ranunculus*, Monkshood, *Corydalis*, *Eranthis*, *Leontice*, *Bunium*, *Smyrnium perfoliatum*, and *Chærophyllum bulbosum*, do not in the first year after germination go beyond the formation of green cotyledons; green shoot-leaves are not developed from the bud or plumule until the next year. Many plants, on the other hand, unfold green shoot-leaves almost simultaneously with the cotyledons, but the cotyledons function with them as foliage, and sometimes remain fresh and green until the time of flowering, or even until the ripening of the fruit. Examples of these are afforded by numerous quick-growing annual weeds in our fields and kitchen-gardens (*e.g.* *Fumaria officinalis*, *Scandix Pecten-Veneris*, *Arnoseris pusilla*, *Urtica urens*, *Adonis æstivalis*). The cotyledons, in rapidly-developing annuals, sometimes attain dimensions scarcely inferior to those of the green shoot-leaves. For example, the cotyledons of the Gourd are more than a decimeter long, and 4–5 cm. broad. It is

to be expected that these green cotyledons, whose function is precisely the same as that of the green leaves of the shoot, should also be protected in exactly the same way against external injurious influences, and as a matter of fact many of the protective contrivances are found on them which have been described in detail previously.

The cotyledons of many Borragineæ are beset with stiff bristles (*e.g. Borago, Caccinia, Anchusa, Myosotis* (see fig. 148 [8]); those of roses are fringed with glandular hairs (see fig. 148 [10]); and those of many nettles bear stinging hairs on their upper surface. It has been already pointed out on p. 350 that cotyledons protect themselves, and the young shoot-leaves hidden between them, against the injury which might happen from loss of heat on clear nights by folding together and assuming a vertical position.

SCALE-LEAVES, FOLIAGE-LEAVES, FLORAL-LEAVES.

When the leaves borne on the shoot were distinguished as scale-leaves, foliage-leaves, and floral-leaves, it was not implied that these three kinds of leaf-structures were actually developed on all shoots. *Scale-leaves* are only found developed on perennial plants. In annual plants they are entirely absent. Even the bud which arises at the apex of the hypocotyl of an annual plant begins at once with green foliage-leaves, nor are traces of scale-leaves to be seen in the buds which are subsequently developed on the epicotyl. Now, what can be the cause of this difference between annual and perennial plants? Obviously annual plants require no scale-leaves. It is of great importance for them that they should develop fruits and seeds in the short period of a single summer; for this they must manufacture the building materials necessary by the help of their green foliage-leaves. A portion of the building materials is employed in the formation of the embryo in the seed; another part in the production of well-stocked food-reserves associated with the embryo. The seeds become detached and scattered, whilst the parent plant which has produced them shrivels up and dies. It leaves no buds behind to persist through the winter and sprout next year; consequently any provision for the maintenance of such buds would be superfluous. It is different in perennial plants, as the buds formed by them must be provided with the necessary reserve-food, and protected during the period of inactivity, throughout the winter sleep and summer rest, against extremities of cold and heat, from freezing, burning, and drying up. They must also be protected as well as possible against the attacks of animals, and these tasks are assigned to the scale-leaves, which serve on the one hand as storehouses for reserve food-materials, and on the other as protective envelopes covering the still short axis with its rudiments of foliage or floral-leaves. Of course no green leaf-blades, and, generally speaking, no green tissue is required for the fulfilment of these functions. The brown or colourless leaf-sheath is sufficient for the purpose; which explains why the scale-leaves appear on all shoots as pale, husky or scale-like structures without green blades. Even the first bud of the plant arising at the apex of the hypocotyl is provided in most perennial plants with pale scaly leaves,

and this is the case not only in woody plants, *e.g.* in the Oak, as illustrated in fig. 144 [5] and 144 [6], but also in quite small herbaceous plants, as in the Moschatel (*Adoxa Moschatellina*), in which small scale-leaves without chlorophyll, followed by green foliage-leaves, are developed above the cotyledons on the epicotyl, and above these floral-leaves. All the shoots (that is to say, buds) developed later on in perennial plants start below with scale-leaves from which the green blade is absent, perhaps because it would be superfluous.

The scale-leaves which are developed on subterranean shoots, especially on bulbs, rhizomes, and turions, differ considerably from each other according to the various conditions of growth of these three kinds of shoot-structures. By bulb (*bulbus*) we understand an erect subterranean shoot, whose very short, thick axis is covered with relatively long, closely-packed, scale-leaves lying one above another. The resting bulb is really a bud, and its form is occasioned almost entirely by the shape of its scale-leaves. These are in most instances broad and concave, and they are arranged so that the inner ones are completely invested by the outer, as, for example, in tulips and species of onion; and they are elongated, ovate, or lanceolate, and lie on each other like the tiles of a roof, as in the lilies (*Lilium Martagon*, *album*, &c.). The adjacent scale-leaves are sometimes united, as, for example, in the Crown Imperial (*Fritillaria imperialis*). Those of bulbs function chiefly as storage-organs. The shoot, whose base they cover, when it begins to develop, withdraws the necessary building materials from this storehouse until its foliage-leaves become green and emerge above the ground; then the leaves are able to manufacture new organic materials in the sunlight. Bulbs are protected against the risk of drying up by the earth surrounding them, but it is very important for them that they should also be protected against the attacks of animals which live underground, and particularly from their nibbling. In addition to the poisonous materials for warding off these attacks, further protection is afforded chiefly by the fact that the exhausted and dead older scale-leaves do not entirely decay and disintegrate, but remain as a sheath. Sometimes they form a tough parchment-like investment, or their thick reticular and latticed strands remain as a sort of cage, within which the young and succulent bulbs are inclosed and protected, as may be particularly well seen in crocuses, gladioluses, and tulips.

The scale-leaves also perform the part of storage-tissues in subterranean, horizontally elongating shoots, called rhizomes or root-stocks (*rhizoma*). They also often serve as protecting envelopes, especially when they cover the apex of the stem as it pushes its way through the ground. In the latter case their cells are strongly turgescent, or more frequently very hard, almost horny, and are folded closely over the apex of the shoot, forming a stiff, pointed cone which is able to penetrate even clayey soil like a borer.

By turion (*turio*) is meant a bud originating laterally on underground stem-structures and developing in the summer into a shoot which rises above the ground. In the autumn its upper part dies off, whilst its lowermost, subterranean portion persists through the winter and originates new buds. Here

the scale-leaves principally function as protecting envelopes for the foliage-leaves. The young and still very delicate foliage-leaves, folded together within the bud, are entirely surrounded and over-arched by them. The sheath-like scales close together like a dome over the bud, and form an actual shield for it. Either hard, much-thickened cells, or more usually, strongly turgescent cells are present at the apex of each of these scale-leaves, and often these coverings are injured in penetrating the soil; but this is not of great importance because the scale-leaves become superfluous and perish when once the foliage-leaves have emerged and expanded above the ground. If earth is thrown up over the underground stock of such a plant as the Rhubarb, the scale-leaves of the turions increase in length in proportion to the thickness of the heaped-up stratum. The growth of the leaves keeps pace with the growth of the enveloped shoot; scarcely has the earth been penetrated when the scale-leaves stop growing, and the shoot—no longer requiring a protection against the ruggedness of the soil—rises up from its sheathing envelope and unfolds its young, green foliage-leaves in the sunlight. If the layer of earth which has been piled up above the subterranean stock is too thick, and if the store of building-materials for the lengthening of the sheathing scale-leaves is inadequate, then the young, green foliage-leaves are forced to leave their protecting envelopes even below the ground, and make their appearance above usually damaged, torn, and mutilated. Many fumitories (*e.g. Corydalis fabacea*) have only a single sheathing scale-leaf which surrounds that part of the shoot possessing green foliage-leaves. Here also it can be plainly seen that the scale-leaf affords protection only as long as it is necessary, *i.e.* the scale stretches up from the lowest portion of the shoot-axis until it has reached the surface of the ground, where the delicate, green foliage-leaves no longer require protection, and can unfold in the air. If the Corydalis is rooted only superficially in the earth, the scale-leaf is raised a very little, often scarcely a single centimeter, but if it is very deeply rooted, or if earth is heaped up over it either purposely or accidentally, then this lengthening of the lower portion of the stem amounts sometimes to more than 20 centimeters. In either case that portion of the stem by which the sheathing scale-leaf is raised stops growing as soon as the apex of the sheathing envelope has reached the surface of the soil, and it looks as if the Corydalis had deliberately adapted itself to the existing conditions.

Many plants have two kinds of underground scale-leaves. Firstly, those whose cells are filled with starch and other food-reserves. These are always thick and fleshy, and they do not continue to grow, but are absorbed by the growing shoots. Secondly, sheath-like ones, which elongate, inclose, and protect the green foliage- or floral-leaves, in their passage through the layers of earth as they grow up towards the light; these do not cease growing nor lose their turgescence until the delicate structures within reach the surface, when they are in no more danger, and require protection no longer.

Scale-leaves situated above-ground are found on the buds of all woody plants, both on foliage and floral buds, *i.e.* both on the lowest portions of those rudimentary shoots which are destined to become leafy shoots, and in those which develop floral-leaves immediately above the scale-leaves. As a rule they present a hard, tough epidermis, are frequently covered externally with adhesive substances, hairs, and the like, and chiefly serve as a protection against the drying up of the little shoot within. When in springtime this axis begins to elongate, they are either immediately detached and thrown off, as in willows, or they may separate just sufficiently to permit the shoot to grow through, as in *Koelreuteria paniculata.* In many species they remain undisturbed and unaltered in their position; in others they separate and remain for some time at the base of the new shoot, as in the Walnut and Ash; whilst in others, again, they are turned back and soon fall off, as in the Mountain-ash (*Sorbus Aucuparia*), and in most species of the Horse-chestnut (*Æsculus*). *Æsculus neglecta* is especially noticeable in this respect, since its bud-scales, which are detached almost simultaneously, are large and red in colour, and when they fall off they cover the ground under the tree quite thickly as if with autumnal foliage. In most instances the scale-leaves on the buds of woody plants are brown and devoid of chlorophyll, and increase in size only slightly during their separation from one another; those of *Gymnocladus,* however, have a green colour, and increase in the spring to twice or even three times their former size.

On the buds of willows only a single scale-leaf is to be seen; limes have two, alders three, manna-ashes four, while in the beech, hornbeam, elm, and *Celtis occidentalis* there are very many bud-scales. If only a single scale exists, as in willows, it is deeply hollowed, and surrounds the part of the bud to be protected like a husk. If only a few scale-leaves are developed, as in *Gymnocladus,* they arch like a dome over the young green foliage-leaves; but if many, then they lie close above one another like the slates of a roof. It remains yet to be noticed that in all cases where the bud is protected by a single or only a few scale-leaves, their texture is always very tough and hard; but where many are present they are thin and membraneous. It has been previously mentioned that the stipules of many plants, as, for example, of fig-trees, magnolias, and the tulip-tree (fig. 91), take the place of scale-leaves as protective coverings.

Foliage-leaves, unlike scale-leaves, exhibit an almost inexhaustible variety in their internal structure and external form, a fact partly due, no doubt, to the multifarious duties they have to discharge. The most important of all these functions is the manufacture of organic materials from inorganic food—on the efficient discharge of which the existence, not only of individual plants but of the whole organic world depends. This almost entirely devolves upon the foliage-leaves. Of course, in numerous instances cotyledons and floral-leaves, the cortex of branches, and in some plants even aërial roots discharge this function; but all these are so subordinate that we may say that more

than 90 per cent of the organic matter manufactured throughout the whole world every year should be reckoned to the account of the green foliage-leaves.

That those members of the plant to which is allotted the manufacture of organic matter should exhibit such a marvellous diversity can hardly astonish us. For how infinitely varied are the conditions under which this function is performed in the different zones and regions of the globe! Even within the narrow confines of a restricted area, one may find habitats damp and dry, sunlit and shady, tranquil and tempest-tossed. Nor should we be surprised to find leaves of diverse shape at different heights on one and the same shoot, and that the foliage borne by any plant may exhibit variations in form in successive seasons of the year. And then we must remember that besides the most important function mentioned, foliage-leaves have often to provide for the irrigation of rain-water to the absorbent roots, to play the part of climbing organs, or to serve as weapons; more than this, they even act as organs for digesting imprisoned animals, with which last function is associated very curious metamorphoses of foliage-leaves. By the segmentation of the leaf into those parts, into the blade, leaf-stalk, and sheath with stipules, an allotment of these various functions becomes possible; but evidently, in consequence of this division of labour in one and the same leaf, the structure becomes much more complex and manifold.

A distinctive name has been given to each shape by botanists, who have endeavoured to define the different forms by descriptions. For foliage-leaves alone perhaps a hundred different expressions have been used to shortly designate the most remarkable varieties. Since these terms of botanical nomenclature can be combined and varied according to the actual facts, we are able to describe the many thousands of differently-shaped foliage-leaves, briefly and tersely, and—what is of especial value, and really the most important aim of these descriptions — another person is able from them to picture the object to himself.

First of all, let us describe the leaf-blade, the outline of which may exhibit every imaginable geometrical form: obovate, circular, elliptical, rhombic, rhomboidal, triangular, pentagonal, &c. Very often, too, the leaf-blade is much elongated, and the margins are parallel to one another; this is known as linear. The free end of the blade is sometimes pointed, sometimes blunt, and sometimes drawn out into a long point; occasionally, again, it is truncate, pressed in, or cut out in the form of a heart. The base of the leaf-blade may be narrowed and attenuate towards the stem; or its outline may be kidney-shaped, arrow-shaped, lanceolate, ovate, spathulate, crescent-shaped, &c. The blade is either undivided, when it is termed entire, or the margin is to a greater or less extent indented; if the indentations are but slight, the leaf-blade is said to be crenate, serrate, or dentate, but if they are considerable, the margin is said to be sinuous or incised; if, again, the indentations go more

deeply into the green surface of the blade, the expressions lobed, cut, divided, or partite may be used. A partite leaf appears as if composed of several leaflets, and such leaves have also been termed compound leaves, especially when the already-described pulvini are present at the base of the individual leaflets.

The distribution of the strands traversing the green tissue is connected in the closest manner with the structure and shape of the leaf-blade. Expressions have been borrowed from the anatomy of the animal body to designate these strands, and they are called indifferently veins, ribs, and nerves. The term "vein" has some justification, since most of these strands contain cells and vessels which serve to conduct fluid materials to and fro; but since there are also strands which have nothing to do with this conduction, which are developed exclusively for the support of the whole blade, the name is unsuitable, and can only be used figuratively. The same may be said of the term "ribs". In many instances the strands in question, of course, do present the appearance of ribs, and the whole arrangement of them in a blade may be compared with a skeleton upon which the soft portions are attached. We even speak of "leaf-skeletons", an expression which seems justifiable, since by removing the soft portions a white framework is obtained exhibiting a great analogy to the bony skeleton of an animal body. Thus if the blades of green foliage-leaves are allowed to macerate for some time in water, the epidermis and thin-walled green tissues decay, while the tougher strands remain intact; if these leaves are now dried and brushed, all the soft disintegrated parts are removed, and only the skeleton of the leaf remains, in which, as in the skeleton of an animal, larger and smaller structures may be recognized, connected together in the most varied manner. But from the fact that most of the strands, together with those cells which serve to strengthen the whole blade, also contain conducting tubes; that many of them indeed consist only of conducting vessels, it is hardly permissible to speak of skeletons, or to apply the term "ribs" to the strands so beautifully interlaced. Finally, the name "nerves" is still more unfortunately chosen, for the strands of leaf-blades have no resemblance to animal nerves, either in structure or function. Consequently this designation must be also condemned, although it is the one most often employed by descriptive botanists.

It is simplest and most correct to call the structures in question what they really are, viz. strands, strands consisting of elongated and fibrous cells, which are combined in the most diverse ways with tubular and pipe-like vessels, and whose elements serve partly for the conduction of fluid materials to and from the green tissues, and partly to afford the necessary protection to the whole blade—protection against strain, pressure, and bending, according to the need of the moment.

In looking for the origin of the strands on a leaf-blade, we are always directed to the stem from which the leaf in question springs. In other words, the first trace of those strands, which traverse the leaf-blade as a richly-articu-

lating system, is already found in the stem. From this they extend through the leaf-sheath and petiole to the base of the blade. This last is therefore in a manner the entrance-gate for the strands, and as soon as they have passed it a division takes place not unlike that of a stream which flows from a narrow valley into a plain, and there breaks up into numerous larger and smaller branches; or they may perhaps be still better compared to an aqueduct whose main stream is inclosed and strengthened by masonry and embankments, but which branch out, at the confines of the town which has to be supplied with water, into several subordinate conduits which penetrate the different districts, and then again break up into numerous smaller water-pipes leading to the buildings and other places of consumption.

We may distinguish two kinds of distribution in respect of the course of these strands as they enter the leaf. In the one case there is only a single thick strand, the primary strand, which distributes itself and breaks up inside the narrow gate. In the other, three or more distinct main strands pass over, side by side, into the blade, each following a separate course. As a rule, these are connected by bridges and inter-networks. Thus we distinguish between leaf-blades with a *single* main strand and those with *several.*

Leaf-blades with one main strand may be sub-divided into two groups according to the form and course of the lateral strands which arise from the primary one. Either these lateral strands are all weaker than the main one, and originate from it successively, at intervals, like the ribs of a spinal column, or like the barbs on the axis of a feather, when we speak of a *feather-like* (or pinnate) arrangement of the lateral strands (see figs. $149^{1, 2, 3, 4, 5, 6, 7, 10, 13}$); or the lateral strands are almost as strong as the main one, arise from it directly at the base of the blade, and run out from this point like rays towards the margin of the lamina. This arrangement of the lateral strand is called *radiating* (see figs. $149^{8, 9, 11, 12}$).

When the lateral strands are arranged like a feather, it generally happens that they are alike in the matter of strength, that they are distributed symmetrically over the whole blade, and originating at fairly equal intervals from the main strand, take, at least at first, a parallel course. More rarely it happens that stronger and weaker lateral strands alternate, and that they diverge from the primary one at unequal angles. In the Camphor Tree (*Laurus Camphora,* fig. 149^{4}), the Cinnamon Tree (*Cinnamomum*), and many other plants related to the Bay Laurel, this peculiarity is found, viz. that two lateral strands which proceed from the lower third of the main one are stronger than the others, looking as though a three-pronged fork had been inserted in the leaf. In the Wall-Pellitory (*Parietaria*), whose leaves show a similar character, stronger and weaker lateral strands alternate, and, strangely enough, the stronger spring from the main strand at an acute and the weaker at a right angle. For the rest, the lateral strands with feather-like arrangement may be distinguished as *reticulate, looped, arched,* and *undivided.*

Those lateral strands are termed *reticulate* (dictyodromous), which break up into a delicate net-work soon after their origin from the primary strand, or at least before they have reached the margin of the blade. The meshes of the net-work are of almost equal size, so that it is impossible to distinguish in the confusion of small strands near the margin of the blade any particular one more vigorous than the others. The leaf of the Wild Pear (*Pyrus communis*) is given as an example of this form in fig. 149[1]. The same distribution of strands, however, is found in very many other plants allied to pear-trees, as also in willows, rhododendrons, and species of barberry and sage.

The lateral strands called *looped* (brachydodromous) run fairly straight and distinct towards the margin, but before reaching it they bend round in a graceful sweeping curve, towards the apex, uniting with the next lateral strand above, and with it form a loop. Such loops can always be seen standing plainly out from the delicate net-work of small strands, and the arrangement may be recognized at the first glance. It is observed in the leaves of the Mahaleb and common Cherry, in the Buckthorn (*Rhamnus Frangula* and *Wulfenii*, see fig. 149[2]), in myrtaceous plants (*Myrtus*, *Metrosiderus*, *Eugenia*, see fig. 149[13]), in many species of dock and nightshade, and especially in rough-leaved plants (Boraginaceæ). The net-work of fine strands inserted between the laterals is often so delicate that it is scarcely visible to the naked eye, and then only a series of bold loops, like arcades, is to be seen in each half of the leaf. In the Comfrey and Lungwort (*Symphytum* and *Pulmonaria*) these loops are developed at some little distance from the margin of the leaf-blade. In the cherry and buckthorn, on the other hand, the loops are quite close to the margin. The lateral strands are frequently very delicate, and extend in a straight line from the primary strand right up to the margin, when they bend suddenly round, like a knee, almost forming a right angle. The outer limb of this right angle then runs parallel to the margin, and unites with the knee of the next upper lateral strand. In this way we have a strand running parallel with the leaf-margin connected with the central primary strand by cross-ties. This looped form occurs very regularly in the Myrtaceæ, but many tropical Moreæ are also distinguished by it, and the leaves of the Forget-me-not (*Myosotis*) also exhibit this peculiar arrangement of lateral strands (see fig. 149[10]).

Arched strands (kamptodromous) are those which run out from their place of origin on the main strand towards the margin of the leaf, which, however, they never reach, but turn in an arch towards the leaf-apex, and there lose themselves without forming definite loops. As a rule, the places of origin are crowded together in the lower half of the main strand, and the two uppermost arched lateral strands then inclose an oval central area. The Cornel (*Cornus mas*), illustrated in fig. 149[3], is chosen as an example of this form.

Those lateral strands are called *undivided* (craspedromous) which run in a straight line from the main strand to the margin and there terminate. They end

either in the apices of the lobes or serrated teeth of the margin, as in hazels, oaks, chestnuts, hornbeams, and hop-hornbeams (see fig. 149 [7]), or in the indentations

Fig. 149.—Arrangement of Strands in the blades of Foliage-leaves. Forms with one main strand.

[1] Reticulate (*Pyrus communis*). [2] Looped (*Rhamnus Wulfenii*). [3] Arched (*Cornus mas*). [4] Arched; the two lowest lateral strands much stronger than the others (*Laurus Camphora*). [5] Reticulate-pinnate (*Populus pyramidalis*). [6] Undivided strands, ending in the incisions of the crenate leaf margin (*Rhinanthus*). [7] Undivided strands, terminating in the projecting teeth of the margin (*Ostrya*). [8] Reticulate (*Hydrocotyle asiatica*). [9] Reticulate strands in the blade of a peltate leaf (*Hydrocotyle vulgaris*). [10] Looped (*Myosotis palustris*). [11] Arched (*Phyllagathis rotundifolia*). [12] Radiate and undivided (*Acer platanoides*). [13] Looped (*Eugenia*).

of the margin, as in Bartsia, Eyebright, and Yellow-rattle (*Bartsia, Euphrasia,* and *Rhinanthus*), and, generally speaking, in all Rhinanthaceæ (see fig. 149 [6]).

Lateral strands with *radiate* arrangement exhibit conditions quite similar to those with a feather-like course. Frequently they are reticulate as in geraniums and mallows, the Judas Tree (*Cercis Siliquastrum*), and many Umbelliferæ, as, for example, in the leaves of *Hydrocotyle asiatica*, illustrated in fig. 149 [8]. In some water-lilies looped lateral strands are also observed, whilst arched lateral strands are very characteristic of Melastomaceæ. In these Melastomaceæ (see fig. 149 [11]) the lateral strands originate from the main strand at the base of the leaf-blade, and travel towards the apex of the leaf in elegant, sweeping arches parallel to the margin. Numerous cross strands, like ties, connect the lateral strands with one another and with the primary one, giving an extremely ornamental appearance to this class of leaf. The leaves of maples exhibit lateral strands radiating towards the margin; this is particularly well shown in the Norway Maple (*Acer platanoides*), the leaf of which is illustrated in fig. 149 [12]. Planes (*Platanus*) also have lateral strands running towards the margin and terminating in the points of the leaf, but it is worthy of remark that in some species the branching of the lateral strands from the primary one does not take place immediately at the base of the blade, but somewhat above it. A peculiar modification of lateral strands with a radiating arrangement is observed in many so-called peltate leaves (see fig. 149 [9]). In these leaves the blade is more or less circular, and is connected with the central stalk as the cover of an umbrella with its stick. The strands radiate out in all directions from the point of attachment of the stalk, and without close investigation of the relations between such a leaf and its petiole, it is often quite impossible to say which of the radiating strands is to be regarded as the main one. This arrangement is found in most species of Pennywort (*Hydrocotyle, cf.* fig. 149 [9]), in Nasturtiums, *Ricinus*, and *Nelumbium*; the last-mentioned plant has also this peculiarity, that its peltate leaves are somewhat depressed in the centre like a bowl.

Leaf-blades with *several main strands* offer far less variety than those with only one. The margin is almost always entire, and they are generally elongated. The most noticeable variations consist in the number of the main strands which enter the base, in their varying thickness, and in the direction which they take in the blade. We have also to consider whether they divide like a fork, and whether the lateral nerves which they give off are developed as cross-connections, or as a fine-meshed net-work.

When the latter is the case, that is to say, when the main strands entering separately into the blade, and travelling towards the apex of the leaf are linked together by a net-work of lateral strands with angular meshes, they are then said to be *apical* (acrodromous). The numerous broad-leaved species of Plantain (*Plantago*), species of Hare's-ear (*Bupleurum*) belonging to the Umbelliferæ, the leaf of one species of which (*Bupleurum falcatum*) is represented in fig. 150 [1], show apical main strands. In the leaf of the Hare's-ear the main strands are crowded together in the narrow base of the blade, and the meshes

of the net-work between these strands are principally formed from transversely-running lateral strands. In the Australian *Leucopogon Cunninghami*, one of the Epacrideæ (see fig. 150 [6]), the very narrow meshes of the net-work are, on the other hand, formed by the longitudinally-running lateral strands. A very peculiar form of the apical arrangement of strands is that which the older botanists called *pedate*. Three distinct strands enter the base of the blade from the leaf-stalk; the central strand is relatively thin and passes

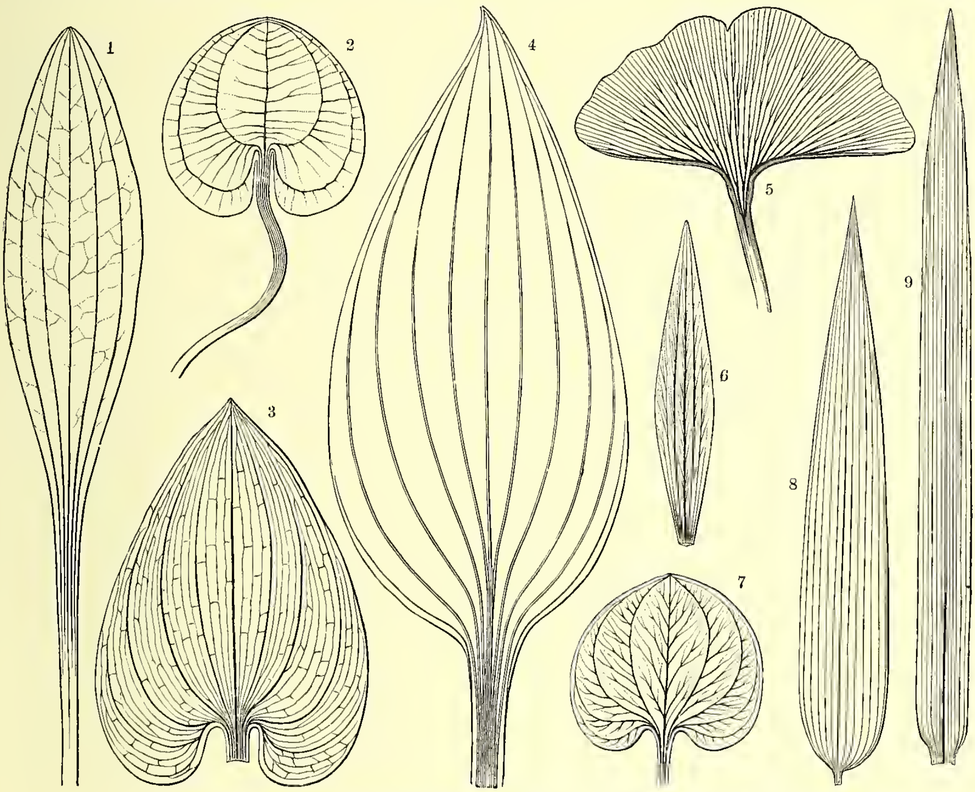

Fig. 150.—Distribution of Strands in the blades of Foliage-leaves: Forms with several main strands.

[1] Apical or acrodromous (*Bupleurum falcatum*). [2] Curved or campylodromous (*Hydrocharis Morsus-ranæ*). [3] Curved (*Maianthemum bifolium*). [4] Curved (*Funkia*). [5] Fan-like or diadromous (*Ginkgo biloba*). [6] Apical or acrodromous (*Leucopogon Cunninghami*). [7] Apical, "pedate" (*Parnassia palustris*). [8] Parallel (*Bambusa*). [9] Parallel (*Oryza clandestina*).

direct towards the leaf-apex; the two lateral are thick, bend round like an arch to the right and left as soon as they have entered the blade, and then send arched lateral strands toward the upper margin, which are almost equivalent to the central main strand, and may at first sight even be taken for main strands. This arrangement is found in the Birthwort and Asarabacca (*Aristolochia Clematitis* and *Asarum Europæum*), in numerous violets and Ranunculaceæ, and in the Grass of Parnassus (*Parnassia palustris*), the leaf of which is shown in fig. 150 [7].

Main strands which enter the blade in large numbers, but always separately,

and of which the external ones travel towards the apex of the leaf in an arch parallel to the margin, are termed *curved* (campylodromous). The lateral strands which are usually so delicate that they cannot be recognized by the naked eye always form spans, connecting the adjacent main strands transversely. In the leaf of the May Lily (*Maianthemum bifolium*) depicted in fig. 150 [3], the number of main strands is very large and the span-like laterals are short. In the leaf of the Frogbit (*Hydrocharis Morsus-ranæ*, see fig. 150 [2]) only five main strands traverse the leaf-blade, the connecting ties being remarkably long and distinct. In Bananas and Scitamineæ (*Musa, Maranta, Zingiber, Canna*) the curved main strands look like arched laterals branching off from a single central strand, but on looking closer it becomes evident that the thick rib traversing the centre of the leaf, like a keel, is not a single main strand, but consists of many separate strands which are embedded in a large-celled mass of tissue. These main strands are inclined one above the other laterally away from the keel, travel towards the leaf-margin and there curve up towards the apex. In bananas this bundle of separate strands, surrounded by parenchyma, extends from the base to the apex; in species of the genus *Funkia* (see fig. 150 [4]) only part way to the middle of the blade.

When several distinct main strands enter the blade from the leaf-sheath or leaf-stalk, running parallel to one another in a relatively wide area without dividing and not converging until the actual leaf-apex is reached, they are termed *parallel* (parallelodromous). Such an arrangement of strands is found in many liliaceous plants, in orchids, rushes, sedges, and especially in the thousands of different grasses. The strands enter the blade either from a broad sheath, as, for example, in *Oryza clandestina* (see fig. 150 [9]), when their separate nature can be easily recognized even at the base of the blade; or they enter by a sort of stalk on which the blade is inserted, as in bamboo leaves (see fig. 150 [8]), where the strands entering the base of the blade appear bent like a knee. Parallel strands are usually of unequal thickness, the central being almost always stronger and more vigorous than the lateral. But even among the lateral, thicker and thinner often alternate in a manner definite for each species. In the slender False Brome Grass (*Brachypodium sylvaticum*), for example, from two to five weaker strands always appear between every pair of stronger ones; the weaker are often so exceedingly delicate that they cannot be recognized by the naked eye. The unaided vision recognizes eleven almost equally thick strands in the leaf of *Oryza clandestina*, represented in natural size in fig. 150 [9]; under a lens five more delicate strands are to be seen between every pair of these. When lateral strands are present, connecting the adjacent parallel main strands, they always take the form of transverse ties.

Finally, we have here to consider that remarkable arrangement of strands which is called *fan-like* (diadromous). A few separate main strands enter the leaf-blade, divide up repeatedly into forked, straight-running branches, and the ultimate twigs terminate at the upper margin of the leaf. This course of the

strands goes with a very peculiar form of leaf, which may best be compared to an open fan. The Maiden-hair Tree (*Ginkgo biloba*, see fig. 150[5]) may serve as an example of this distribution of the strands, which, on the whole, is not common. It is also observed in several true ferns (*e.g. Adiantum arcuatum*, *Acrostichum sphenophyllum*, and *Livingstonei*). With regard to the Ginkgo, it should be mentioned that as a rule only four distinct strands enter the blade from the leaf-stalk; two central which are very delicate, and two lateral which are very strong, and from which arise a large number of fine, forking strands running upwards.

Besides the arrangements of strands in leaf-blades here described, there are many which cannot readily be brought under the limits defined; in the same way there are intermediate forms which may be placed just as well in one as in another of our artificial divisions, and which we try to describe clearly by connecting the technical terms together. For example, we find intermediate forms between arched and reticular strands which are described as arched-reticulate, and so forth.

The fact should be emphasized that the distribution and arrangement of the strands in any given species is remarkably constant. This, however, is by no means the case in genera and families. Of course there are plant-families the whole of whose members exhibit marked agreement in this respect, as, for example, the Rhinanthaceæ, Melastomaceæ, and Myrtaceæ; but, on the other hand, instances are not lacking where the reverse is the case. Thus the various genera of Primulaceæ present the widest varieties, and even the individual species of the genus *Primula* differ more from each other in the arrangement and course of the strands than perhaps the Myrtaceæ from the Boragineæ. Nevertheless the accurate determination and description of the distribution of these strands in the leaves is very important for that branch of botanical study, the object of which is to provide criteria for the discrimination of species. The careful investigation of the distribution of strands in leaves is, perhaps, of the greatest interest to the palæo-botanist, the investigator of pre-existing vegetation. Those parts of plants which have come down to us from earlier periods, embedded in geological formations, consist principally of single leaves or fragments of leaves, often of very insignificant appearance. In these fragments often we cannot even recognize plainly the edge, much less the whole contour of the blade; but the strands themselves, and the net-work which intervenes between the coarser strands, may be distinguished on the smallest fragments. Often enough the palæo-botanist has only such scanty remains to refer to when he seeks information about the species of plants with which our globe was covered in long-past ages. Consequently even the most insignificant-looking bit of leaf-network becomes of the highest importance. Just as an investigator, busy with the history of the human race, can draw certain inferences from the characters of a hardly decipherable papyrus roll about the state of the household, about the political institutions, the customs, manners, and civilization of the population settled more than two thousand years ago in the valley of the Nile, so can the botanist,

investigating the history of plants and attempting to clear up the connection between past and present, recognize from fossil leaves the species living in periods long past, and read the condition of vegetation as it existed many thousands of years ago. Although the results of investigation hitherto obtained in this field are still imperfect, and although these results may receive manifold additions and corrections as more abundant materials come to hand, still the history of vegetation is already exposed in its principal features, and that which has been obtained in this respect during the comparatively short period of half a century is noteworthy in a period of remarkable additions to natural knowledge. In imagination we see replaced the woods and meadows which long ages ago adorned the continents of the Coal period; colonies of slender calamites, the rigid fronds of the cycads, and thickets of countless ferns rise up before us; we are able to sketch landscape pictures of the Jurassic and Cretaceous periods, and to see the banks of the rivers fringed with species of *Cinnamomum*, evergreen oaks, walnut- and tulip-trees. And all these pictures of the vegetation of the most remote periods would hardly have been possible except on the basis of the determination of species with the help of the minutest investigations into the arrangement and distribution of the strands in the fossil leaves.

When the leaves of fossil and living plants are compared, we notice that the strands in the former appear more distinct than in the fresh succulent green blades. This is in consequence of the fact that in living plants the strands are often embedded in parenchymatous tissue so that they cannot be seen on the surface, while in fossil plant-remains the parenchyma has been wholly destroyed and only the strands have been preserved. When the strands run in the interior of the substance of a leaf, and are not visible at the surface, they are hidden, or, to use the technical term, *hyphodromous*. Succulent leaves almost always have such hidden strands, which may be contrasted with those which project above the general level on either side of the leaf. On the whole this latter condition is rare, most usually the strands project on one side only, and that the lower surface. Often we find a plexus of ridges on the under side, and one of grooves on the upper side corresponding to the course of the strands. The enormous circular leaves of the *Victoria regia*, which float on the surface of the water, have very strong projecting ribs on the lower side. In leaves of submerged water-plants, however, the strands are insignificant; many are even destitute of vessels, and present only strands of elongated cells, as, for instance, the leaves of the celebrated *Vallisneria*. This is easily understood, as the need of resisting pressure and bending in submerged leaves is very slight. Nor do submerged plants require special conducting tubes for their food-salts. Numerous other striking relations existing between the inner structure of the leaf-blade and the peculiar conditions of the habitat of plants have already been discussed, and we need here merely refer to the description of flattened, rolled, succulent, spiral, arched, hinged, and tubular leaves occurring in the section which begins on p. 209 of this volume.

The form of the leaf-stalks, stipules and leaf-sheaths, in their dependence on

the peculiar conditions of the environment, has also been repeatedly discussed, and it is enough to remember here that the principal duties of the leaf-stalk, as the support of the light-needing green blade, are to turn and twist it, to raise and lower it, to bring it always into a position where it will be properly illuminated; to keep it in that position in spite of storm and tempest. The chief function of stipules consists in screening young and tender leaves—not yet emerged from the bud—from excessive illumination, and protecting them from too much loss of heat on clear nights. The stipules in many cases actually serve as bud-scales, as may be seen in the fig-tree, where the tiny leaf-blades are rolled up together and inclosed in the spathe-like stipules. When this is the sole function of the stipules, they become detached after the unfolding of the leaves wrapped round by them. Consequently, shortly after the unfolding of the foliage of oaks, beeches and other trees, the floor of the forests formed by these trees is strewn with enormous quantities of fallen stipules. When the stipules persist at the sides of the leaf-stalk and become green, there can be no doubt but that they supplement the green leaf-blades in their function, and like them manufacture organic substances from inorganic food. In the Woodruff, Bed-straw, Madder (*Asperula, Galium, Rubia*) the stipules actually possess the same size, shape and colouring as the blades of the real foliage-leaves, and thus a star of green leaf-structures is formed, to which these plants owe their name of Stellatæ. In the Pansy (*Viola tricolor*) and numerous species of violet allied to it, the stipules are green and sometimes larger than the leaf-blade, at the base of which they occupy a subordinate position.

A peculiar formation is observed in the Yellow Vetch (*Lathyrus Aphaca*), a common weed in the fields of Southern Europe, though not so frequent in England. In this plant the leaves are completely transformed into tendrils which serve as climbing organs; the two stipules which stand at the base of the metamorphosed leaf have, on the other hand, assumed the function of leaf-blades; they are very large, provided with green tissue, of arrow-like or lanceolate contour, and at a cursory glance may be easily taken for leaf-blades. It has already been mentioned on p. 335 that a like modification of function occurs in many Australian acacias, the foliage-leaves of which are devoid of green blades whilst the leaf-stalks are developed as green, flattened, outspread organs, the so-called phyllodes.

In all these cases we have only treated of the most important function of foliage-leaves, that is, the formation of organic materials from inorganic food in sunlight. But as mentioned previously, the foliage-leaves of many plants are assigned other functions, which again require certain peculiar adaptations, and contribute not a little to the great variety in the form of this organ. One series of these metamorphoses, viz. the transformation of the leaf-blades and leaf-stalks into traps and digestive organs in insectivorous plants; the metamorphosis of blades, leaf-stalks, and stipules into weapons; and the development of furrows and channels on different parts of the foliage-leaves for the irrigation of rain-water; and finally the transformation of foliage-leaves into mere scales, as in the switch plants, &c.—all these have already been fully treated of in earlier chapters. But

a further series of such transformations, especially the metamorphosis of parts of foliage-leaves into tendrils, hooks, and claws, with the help of which the stem is able to climb up firm supports towards the light, and the transformation of the leaf-sheaths into mechanisms for protecting flowers against unbidden guests; the consideration of these must be deferred till we deal with climbing contrivances and protections for flowers in general; here, there only remains to be considered the production of floating contrivances in certain marsh and water plants, and the development of special cells to assist those foliage-leaves which are unprovided with scale-leaves in breaking through the soil.

Floating arrangements occur in only a few species of plants, most noticeably in the Brazilian *Pontederia crassipes*, and in the few species of the water-chestnut (*Trapa*). In both instances the leaf-stalks are swollen up into floats, and remind one to some extent of the swollen utricular leaf-stalk of *Cephalotus*, *Sarracenia*, and of pitcher-plants. They are distinguished from these by the fact that the buoy-like swelling is quite closed, and that the partitioned interior neither contains digestive organs, nor is beset with spines, &c., to hinder the exit of imprisoned animals. *Pontederia crassipes* is not fixed in the mud beneath the water by roots, but the plants float freely on the surface of the pond. It is of great importance to these plants that they should have a small specific gravity, and that their leaves, grouped in rosettes, which have been unfolded above the water, should offer a large surface to the air, while at the same time the illumination of the green portions should not be encroached upon. Both these requirements are met by the bladder-like leaf-stalk, and these strange floating plants are driven by the wind like ships hither and thither over the surface of the water.

The plants of water-chestnut are held fast to the muddy bottom under water by roots, and are not adapted to floating freely. The submerged leaves are finely divided like a comb, and have such a small specific gravity that when detached from the stem they immediately rise to the surface of the water. The uppermost leaves lying on the surface of the water, and grouped into rosettes, have rhomboidal, tough, almost leathery blades, and these also do not sink when they are isolated, and therefore it is difficult to see what advantage is afforded in this instance by the swollen leaf-stalk. But when in the height of summer large heavy fruits are seen to be produced from the flowers developed amongst the leaves of these floating rosettes, it then becomes evident that the floating capacity of the rosette-leaves must be maintained, lest they be drawn underneath by the weight of the nuts and placed in a position as unfavourable as could be imagined for the proper discharge of their functions.

In the subterranean buds of perennial plants the rudimentary foliage-leaves are usually surrounded by scales, which function as shields and screens, and in particular play the part of protective organs in the work of breaking through the ground. Most of these sheath-like scales, as already stated, grow up with the elongating buds until the soil has been pierced, and their points strengthened by turgid cells serve as actual earth-breakers. But in some plants which survive through

the winter, with underground buds or bulbs, the young sprouting foliage-leaves do not have this assistance; they must carve their way through the soil unaided, and press above the surface without a sheathing envelope. Accordingly they have to bore through a more or less thick layer of earth, often a stiff clay; or one perhaps containing pointed stones and angular grains of sand. Now in order that the foliage-leaves traversing this rugged and uneven path may suffer no damage, they are variously folded and twisted together so as to form a cone; and most important of all, the apex of this cone, which operates like a ground-auger, and therefore exercises a strong pressure on the soil, is armed with special cells. These cells have a great resemblance to those at the apex of the sheath-like scale-leaves, and to those of the knee-shaped bent cotyledon of the onion (see p. 606). In many plants possessing lobed or deeply-divided leaf-blades, the boring apex of this cone is formed by a bend of the leaf-stalk, which is doubled over like a hook. Thus in the foliage-leaves of the Yellow Monkshood (*Aconitum Vulparia, Lycoctonum*, &c.) it is not the apex of the leaf which emerges first from the ground but the convex part of its bent and knee-like stalk. As long as the leaf is still occupied in boring, the delicate free apices of its lobes are directed inwards and downwards, and not until the hooked leaf-stalk has emerged above the surface of the soil does it straighten and draw the leaf-blade out of the ground. The free points of the leaf-blade, which were hitherto directed downwards, are inclined in the opposite direction when they arrive above the earth, and the whole leaf then unfolds into an expansion parallel to the surface of the ground. An exactly similar process is observed in large ferns with underground winter buds, *e.g.* in the common Male-fern (*Aspidium Filix-mas*). The fronds at the end of the root-stock are spirally rolled, their delicate segments are packed closely together, one above the other, and covered by the strong rachis of the leaf as by a thick hoop. Only the back of this rachis comes into contact with the forest soil as it is broken through; the rachis prises up the top layer of the soil in its gradual unrolling, and the delicate segments are only unfolded when the part of the axis in question has emerged and straightened itself.

The earth is broken through in a very peculiar manner by the peltate leaf-blades of *Podophyllum peltatum*. As long as the leaves of this plant are still small and below the ground, they resemble a closed umbrella; the folded blade is directed downwards, and nestles close to the thick stalk, which grows straight up. At the free end of the stalk, which would correspond in position to the ferule of an umbrella held upright, is found a group of thin-walled, turgid cells, without chlorophyll, situated like a white knob at the converging-point of the leaf-strands. When the leaf-stalk grows in height, it is this cell-group which presses on the layers of earth above it, and it is the first to appear at the surface. The leaf-blade, still furled to the stalk, is then raised up through the hole thus bored. Once above the surface, the blade expands just like an opening umbrella. The above-mentioned group of cells, having served as a buffer, now loses its turgescence, but remains visible as a white spot at the centre of the brownish-green expanded leaf-blade. In the species of the genera *Acanthus* and *Hydrophyllum*, which are characterized by divided leaves,

the lobes of the blades whilst still under the ground are depressed as in *Podophyllum*, but here the penetration is accomplished by means of peculiar bumps and bladder-like protuberances on the uppermost lobes, which again consist of strongly turgid cells. In the Asarabacca (*Asarum*) it is the apex of the lower leaf folded together lengthwise which is composed of turgescent cells, and which growing upwards, presses the earth apart like a wedge. In the Broad-leaved Allium, Dog's-tooth Violet (*Allium ursinum* and *Erythronium Dens Canis*), in the Star of Bethlehem and Hyacinth, and many other bulbous plants, also in numerous orchids of our meadows and woods whose buds pass the winter embedded in deep soil, the apex of the lowest leaf-blade is transformed into an actual ground-auger, usually shaped like a hood or folded cap-like over the apices of the other leaf-blades of the plant. A group of cells without chlorophyll is always found on the apex of that leaf which envelops the others, and this apex may be plainly distinguished by its white colour. In most of the plants examined the cells are thin-walled but very turgid; only a few present thickened walls, as, for example, the Broad-leaved Allium (*Allium ursinum*), where the whole leaf-apex is almost horn-like. This group of turgescent cells always forms the apex of the leaf-cone growing out from the subterranean bud; afterwards when this cone has grown up, and the leaves are spread out over the soil, the formerly tense cells of the leaf-apex collapse, dry up and present a withered appearance. In the Asarabacca and in many orchids the apices of the mature and lower leaves are regularly browned, and look as if burnt, even when they have not been actually injured in penetrating the ground.

The term *floral-leaves* comprehends all those which are directly or indirectly concerned in the processes of fertilization, and in the production of the embryo. First of all we have the leaf-structures within which the germ-cell is formed, that cell from which the embryo proceeds after fertilization. Then there are those in which arise the fertilizing cells known by the name of pollen-grains. Finally all those which are concerned in bringing about the union of the pollen-cells with the germ-cells, or whose task is to protect these two kinds of sexual cells during their development from injurious external influences. Since the processes only shortly indicated here will be fully described in the second volume of *The Natural History of Plants*, and since the forms of the floral leaves will be considered in these descriptions, we need not here give a detailed representation of these structures. In the pages which follow they will only be treated of so far as is necessary for the comprehension of the architecture of the whole plant, and of a series of botanical terms.

With regard to the succession and arrangement of floral-leaves, it has to be noticed as one of their most characteristic features that the last and uppermost floral leaves are always very close together, and are usually developed as closely appressed whorls. These assemblages of floral-leaves together form the *flower*. The axis which bears the flower at its free end is termed the *flower-stalk* (*pedunculus*).

The axis which is terminated by the flower is only in rare instances, viz. in a few annual herbs, the direct continuation of the shoot which is produced from the

first bud (plumule) situated above the hypocotyl (cf. fig. 2). In this case the floral leaves, collected together to form the flower, follow directly above the foliage-leaves on the same shoot. Such a flower is called *terminal*. Much more frequently the flowering axis or peduncle is inserted laterally on an older shoot, and originates close above a leaf, called a subtending leaf; here we speak of *lateral* flowers. Usually several flowers are grouped in a definite way, and the term *inflorescence* (*inflorescentia*) has been introduced to distinguish these groupings. The *subtending leaf* (*folium fulcrans*) either agrees in general character with the lower foliage-leaves, and is then said to be "leaf-like", or it differs in shape and size as well as in colouring, and is then spoken as a *bract* (*bractea*).

These leaves, differing from foliage-leaves, always have a special relation to the processes of fertilization; and are therefore to be reckoned with the floral-leaves. Frequently a whole inflorescence is surrounded and supported by a single enormous bract, and in such inflorescences, which are very characteristic of palms and aroids, the bracts at the base of the individual flower-stalks are usually undeveloped. This large common bract is called a *spathe* (*spatha*). The Climbing Palm (*Desmoncus*) illustrated in fig. 157 [3], has such a spathe beset with prickles. It sometimes happens that some of the flowers of the inflorescence do not develop, and that then bracts are to be seen without flowers. If such "empty bracts" are found crowded together at the base of the inflorescence arranged at one level, or are there grouped in very close spiral revolutions, we speak of an *involucre* (*involucrum*). Sometimes they are to be seen at the apex of the whole inflorescence, the group forming what we may call a *crest*. Minute, stiff, dry bracts, without chlorophyll, in the centre of thickly crowded inflorescences are called *paleæ* (*paleæ*).

In flowers we distinguish perianth-leaves, stamens, and carpels. The *perianth-leaves* are arranged either spirally or in whorls. The former arrangement is observed most noticeably in the cacti, of which a species, the "Queen of the Night" (to be described later on account of its blossoming at night, and of various other interesting features) is illustrated in the Plate VII. here inserted. In the flowers of this plant more than a hundred perianth-leaves are so arranged at small vertical intervals along a spiral line that the smallest stand lowest, the largest uppermost, not unlike the leaves of the involucral cup around the capitulum of a composite. This spiral arrangement, however, is rare, at least in such a striking form. Much more frequently the perianth-leaves form two successive whorls. If the lower whorl consists of green leaves, which agree in texture and in general appearance with foliage-leaves, while the upper is composed of more delicate leaf-structures displaying all possible colours except green, the lower is called the *calyx*, and the upper the *corolla*. If all these perianth-leaves are shaped and coloured very much alike, so that there is no marked contrast between the whorls, we then speak of a *perigone* (*perigonium*). This may be either green like a calyx, or coloured like a corolla.

The *stamens* (*stamina*), the "attire" of the older botanists, are, like the perianth-leaves, usually whorled, or, more rarely, arranged in spirals. Each stamen

consists of the *anther* (*anthera*), *i.e.* that part in which the pollen is developed, and of the support to this anther, which is usually threadlike, and bears the name of *filament* (*filamentum*). Filaments and anthers, in many instances, correspond to the sheathing-part and stalk of the leaf, and in these stamens the blade is wholly suppressed; in other instances the anther is to be regarded as the lower part of the blade, and then the apex of the blade appears as a scale-like appendage. The blade of the stamen sometimes resembles a perianth-leaf, and this is a case to which there will be frequent allusion.

The *carpels* (*carpophylla*) are arranged, like the perianth-leaves and stamens, sometimes in whorls and sometimes spirally. In one section of flowering plants they are scale-like, and present free margins not joined together. In another section they are rolled together and their margins fused, so that a capsule called the *pistil* (*pistillum, ovarium*) is formed. If many carpels are present in one flower, each of them may form a separate ovary, and then the more or less numerous one-leaved ovaries appear arranged either spirally or in a stellate manner as the termination of the shoot in the centre of the flower, *e.g.* in the Ranunculaceæ and Dryadeæ. In the Papilionaceæ and several others allied to these groups of plants there is only a single one-leaved pistil at the end of the flower-shoot; but usually several whorled carpels are united together to form a single ovary in the centre of the flower. A great number of different constructive plans of many-leaved pistils are distinguished according to the manner and extent of union, and these in particular afford excellent marks for characterizing the families and genera. The most striking differences are produced by the whorled carpels being at one time fused with one another along their whole length, while at another, the fusion is restricted only to the lower part; by the fact that frequently the rolled united margins of the adjoining carpels become partition-walls in the interior of the pistil, resulting in the formation of compartments, while in other cases this formation of septa does not occur, the carpels adjoining one another like the staves of a cask, and forming an unchambered capsule.

The *pistil* may be divided into the *ovary* (*germen*), *style* (*stylus*) and *stigma* (*stigma*). The ovary corresponds to the sheathing portion, the style to the stalk, and the stigma perhaps to the blade of the leaf. The ovary forms in most cases an expanded structure; its contour and surface offer little variety, especially when compared with the inexhaustible diversity of other parts of the flower. Usually its shape is ovate, ellipsoidal, spherical, or disc-like, more rarely elongated, cylindrical, or barrel-shaped; sometimes it is flattened from side to side, and has the form of a sword or sabre. Projecting knobs, cushions, angles, ridges, and bands are often found on its circumference in accordance with the number of the carpels of which it is composed, and three- or five-sided forms are met with very frequently. The hairs, bristles, spines, and wings appearing so noticeably on the ovary when it has been transformed into the fruit-capsule are usually so undeveloped at the time of flowering that perhaps not even the rudiments of these outgrowths can be recognized.

QUEEN OF THE NIGHT (CEREUS NYCTICALUS).

Printed from the originals by the BIBLIOGRAPHISCHES INSTITUT, Leipzig.

The ovary contains structures which, from analogy with the eggs of animals, have been termed *ovules* (*ovula*). They are also called "seed-buds", as the seeds are produced from them after fertilization. Formerly the name "germ-buds" was frequently employed for these structures. Those botanists who endeavour to refer the infinitely manifold members of plants to a few fundamental forms, and especially to settle whether a certain structure is to be considered as a stem or a leaf, have fought very much over the ovules. First of all, ovules were regarded without exception as stem-structures, as parts, that is, of the axis, and the uppermost portion of the stem which bears the ovules—or from which the supports of the ovules branch off — were designated as fruit-axes. It was thought that these fruit-axes divided up in the most varied manner, and that they sometimes also became leaf-like, resembling flattened shoots, in which case the ovules would arise from the margins of the flattened expansion. It was also supposed that such fruit-axes might be united with the carpels, and the impression would then be given that the ovules were produced from the carpels. Later, the ovules of all plants were interpreted as leaf-structures, *i.e.* as parts of the carpels, and their direct origin from the axis, that is, from the stem, was denied. Even those ovules which are situated on the apex of the axis, projecting into the centre of the ovarian cavity, were regarded as outgrowths of the carpels, and it was supposed that a freely-ascending, ovule-bearing column projecting into the cavity of the ovary rose up from the base of the united carpels. Various other forced explanations have been given, but it is hardly suitable to consider them here.

These false interpretations are corrected when we no longer lay that stress on the difference between stem and leaf, which was asserted by the advocates of the two views quoted above, and when we remember that really all leaves are produced from a stem, and that it is by no means easy to settle where the stem ceases and the leaf begins. If we rigidly adhere to the history of development and to the actual fact rather than to those speculations on which is based the conception of an "ideal plant", and if at the same time we set ourselves against the attempt to refer all plans of construction to a single fundamental ground-plan, we arrive at this result, that in many cases the ovules proceed directly from the apex of the stem, and that even in the earliest stages of development they have no organic connection with the carpels. They stand in the same relation to the stem as carpels do, and there is no reason why they should not, like them, be regarded as peculiarly metamorphosed leaves. They form the last uppermost leaves originating from the axis, become subsequently a constituent of the fruit, and may also be looked upon, in consequence, as upper carpels. In such instances as these, two successive whorls of carpels are developed, one situated below, whose members develop no ovules, and one placed above, whose members are only formed of ovules and their supports. The lower carpels, without themselves developing ovules, form the capsule arching over the upper carpels which have been reduced to ovules. This view receives the more justification from the fact that similar conditions are observed in the stamens; that

is to say, there are flowers in which the outer lower stamens are flat, leafy expansions, whilst the upper are reduced to anthers and filamentous supports. Of course this is only a view which it would be unwise to insist upon after the foregoing strictures.

This supposition does not exclude the fact that in many instances a single whorl of carpels is developed, and that the carpels of this whorl not only form the capsule, but that at the same time ovules may arise from them. At one time the teeth of the margins of these carpels become ovules; at another, whole segments of a leaf are metamorphosed into ovules; again, in another instance, groups of cells have given rise to ovules over the midribs of the carpels; and lastly, innumerable ovules may have developed from the whole inner surface of the carpels.

The internal structure of the cavity of the ovary is still further complicated by the fact that the end of the axis in one case rises up like a hemisphere or truncated column in the centre of the capsule, while in other instances the end of the axis is hollowed into a pit, and sometimes even deeply excavated. In consequence of these manifold arrangements, very different relations between carpels and axis naturally follow, and the most various constructive plans result, which, however, will be more suitably discussed in the second volume when considering the individual families, especially the Primulaceæ and Onagraceæ.

In whatever way the ovules may be explained, they exhibit a great agreement in structure. In them may be distinguished the *nucellus* (*nucleus*), surrounded by two, or less frequently by only one *coat* (*integumentum*), and also the portion by which the ovule is connected with its substratum, the placenta. Usually this has the form of a stalk or filament (*funiculus*), and then the ovules appear, as it were, suspended in the interior of the ovary. When the ovule is straight, and is a direct continuation of the funicle, it is called *orthotropous*; if the straight ovule is hung on a thread-like support, but reversed, and more or less fused with the support, it is said to be inverted or *anatropous*; when it is curved, the designation *campylotropous* is used. The coats do not completely inclose the ovules, but at one pole a spot which bears the name of *micropyle* is left uncovered.

As already remarked, the style corresponds to a leaf-stalk as regards its position and relation to the other portions of the pistil. In the one-leaved pistil its form frequently resembles a leaf-stalk, especially in papilionaceous plants. If the ovary of a one-leaved pistil be regarded as arising from the sheathing portion, and the style from the stalk of a leaf, it will be easily conceived that the style appears to be affixed to one side of the ovary. The lateral position of the style can be clearly understood if we imagine that the sheathing portion of the ovary is swollen up like a vesicle, as it is on the foliage-leaves of Umbelliferæ, or that it bears large stipules as in the Cinquefoil (*Potentilla*). In the one-leaved ovary of the cinquefoils the style in fact is not seen to spring from the apex of the ovary, but looks as if it had grown out laterally from its capsule. In pistils which are built up of many carpels arranged in a whorl, and having

only their sheathing portions fused, as, for example, in the Meadow Saffron (*Colchicum*), or in the much-cultivated "Love in a Mist" (*Nigella Damascena*), the styles are separate and always fixed at one side of the compartment of the ovary corresponding to them. But when several whorled carpels are completely united with one another as far as the stigma, only a single style is to be seen. This style, which may be considered as a combination of several grooved leaf-stalks, then rises up above the centre of the many-chambered ovary. Just as the leaf-stalk may be frequently absent from foliage-leaves, so sometimes the pistil has no style, and the stigma is sessile or seated immediately upon the ovary.

The stigma corresponds to the blade portion of a leaf, but is expanded in only a few families of plants, amongst which the irises are the best known. It has to receive and hold the pollen-grains, and its form varies according as to whether these are carried by the wind as flower-dust or are brought to the flowers by insects in cohering masses. In the former case the stigmas are brush-like or feathery, often extended like a cobweb or spread out like a plume; in the latter case, projecting papillæ, knobs, ridges and bands are found on them, against which the insects knock off the pollen as they enter the flower.

If we consider now the functions of the various floral structures rather than the position and succession of the individual members, we arrive at the following result. Of all the structures known as floral-leaves the ovules and pollen-grains (*i.e.* those parts of the flower on which these structures are produced) alone are indispensable. These portions of the flower, however, must be protected not only during their development and at the moment of fertilization against possible external injurious influences, but the union of pollen-grains with ovules must be brought about by a suitability in the form of the floral-leaves in addition to the mere production of these bodies. In order to be able to fulfil these tasks the floral-leaves which develop ovules or pollen are themselves often suitably equipped and adapted, or a division of labour takes place, so that only one portion of the floral-leaves develops ovules or pollen, while the other exists for protection and as a means of ensuring fertilization. In many plants, for example, the carpels are not only the bearers of the ovules, but also at the same time their protectors, and by the peculiarity of their structure they conduct the pollen to the ovules they bear. In numerous other plants, on the contrary, a division of labour has occurred; the ovules spring from the axis as independent structures, and the carpels proper surround and protect them, and receive the pollen for them, as may be seen typically in the flowers of primulas. In the American *Pachysandra*, in the Persian *Halimocnemis*, and in many other plants, the stamens produce pollen in coherent masses, but some of them are also provided with allurements for those insects which carry the pollen from flower to flower, and distribute it to the suitable stigmas. A division of labour is met with in most of these plants which have coherent pollen, two, three, or more whorls of stamens are developed, the upper bear anthers and produce pollen, the lower are without pollen, but assume the function of attracting insects and of protecting the upper anther-bearing stamens. Regarded from this

stand-point the perianth-leaves are, as it were, only antherless stamens, and this view is supported by the fact that in the so-called double flowers the anther-bearing stamens regularly change into antherless perianth-leaves. In the flowers of water-lilies as a rule no sharp limit can be drawn between stamens and perianth-leaves, but a gradual transition from one to the other may be plainly noted. The flowers of certain limes (*Tilia Americana, alba, argentea*), as well as those of the arrow-grass (*Triglochin*), of which an illustration is given below, are very instructive in this respect. In the Silver Lime (*Tilia argentea,* figs. 151 [1] and 151 [2]) a whorl of

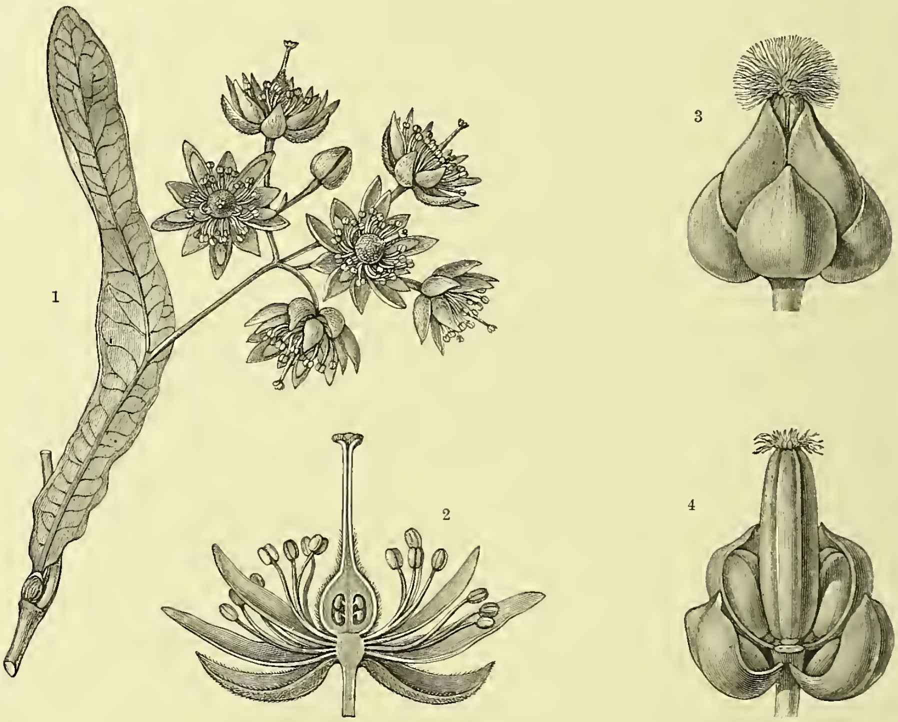

Fig. 151.—Flowers of the Silver Lime (*Tilia argentea*), and of a species of Arrow-grass (*Triglochin Barellieri*).

1 Inflorescence of the Silver Lime, natural size. 2 Longitudinal section through a single flower. 3 Flower of the Arrow-grass, in the first stage of blossoming. 4 The same flower in a later stage of development; one of the upper perianth-leaves cut away. 2, 3, and 4 are enlarged.

stamens with anthers is first formed below the pistil, followed by a whorl of leaves without anthers, which, however, secrete honey to allure insects; then again comes a whorl of leaves with, and below these again two whorls of leaves without anthers. The same is the case in *Triglochin,* whose flowers look as if they were composed of two stories standing one above the other, quite similarly arranged (see figs. 151 [3] and 151 [4]). The flower commences below with a whorl of three hollowed antherless leaves; above these comes a whorl of three leaves with anthers, and the large anthers are surrounded and protected during development by the hollowed leaves as if by a hood; then again follows a whorl of three hollowed antherless leaves, and above these yet again a whorl of three stamens with large anthers, an

arrangement resembling that of the lower story. When the powdery pollen falls from the anthers it is not immediately carried away by the wind, but falls first of all into the hollow cavities of the leaves below the anthers, where it remains deposited until the proper time has arrived for its transmission to the stigma of another flower. These hollowed leaves, although themselves antherless, are therefore filled with pollen for a time, and look like anthers which have just dehisced. They are of the greatest importance for the timely distribution of the pollen and for the accomplishment of fertilization, and may be regarded with respect to the part which they have to play as antherless stamens.

Usually all these leaf-structures of the flower originating from the axis below the pistil and bearing no anthers are designated as perianth-leaves—as calyx- and corolla-leaves, or, lastly, as staminodes. What descriptive botanists understand by perianth, calyx, and corolla has been already described on p. 641; with regard to the term staminode, it should be mentioned that it is applied to all such antherless leaves as are inserted between the whorls of perianth or corolla leaves on the one hand, and the carpels on the other; *i.e.* they occur where in most instances the anther-bearing stamens are placed. Staminodes resemble the stamens very much in shape, but are distinguished from them by the fact that they develop no pollen. They, however, make themselves useful in other ways. Thus in the transmission of the pollen, they secrete honey and allure insects; or they may serve as protective agents for their neighbours, the anther-bearing stamens, against various external injuries. A detailed description of the part performed in the process of fertilization by all these floral leaves which are so differently shaped and are arranged in such manifold ways with regard to one another, is reserved for the second volume of this work.

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3. FORMS OF STEM STRUCTURES.

Definition and Classification of Stems. — The Hypocotyl. — Stems bearing Scale-leaves. — Stems bearing Foliage-leaves.—Procumbent and Floating Stems.—Climbing Stems.—Erect Foliage-Stems.—Resistance of Upright Stems to Strain, Pressure, and Bending.—Floral-Stems.

DEFINITION AND CLASSIFICATION OF STEMS. THE HYPOCOTYL. STEMS BEARING SCALE-LEAVES.

In certain seeds consisting of rounded or ellipsoidal masses of tissue, the embryo shows no obvious division into stem and leaf; nor can any distinction be recognized between the embryo and the surrounding seed-coat. When such seeds begin to germinate, as, for example, those of orchids, their cells become partitioned and multiply, and the whole tissue-body increases in size, but for a long time no trace is visible of a division into stem and leaf. It is shown by the development of the seed of *Cuscuta*, described and figured on p. 173, that the embryo, the seed-coat and the reserve tissue which nourishes the embryo for a time and provides it with the

necessary building materials, may all be distinguished from each other; but the embryo itself shows no segmentation into axis and leaves. It looks to the naked eye like a filamentous, spirally-rolled structure, which breaks through the envelope of the seed-coat on germination, extends and elongates, then grows up straight and afterwards twists and winds and seeks for a resting-place from which it can derive nourishment. This thread may, without further discussion be considered as a stem although it bears no leaves, and indeed never presents even the rudiments of leaves. Not until later, when this thread-like stem has developed haustoria at the spots where it is in contact with the host-plant, and has grown still longer by the help of the absorbed nourishment, do small scales which must be interpreted as leaves arise below the growing point (*cf.* fig. 35 [1] on p. 175). Projections are then developed above the scales which grow out into lateral shoots.

The fact that stems exist, which, in their young condition exhibit neither leaves nor even the rudiments of leaves, is specially emphasized here, because it has been repeatedly denied that the stem is a special member of the plant. This may of course seem strange to the uninitiated, and it will be asked, how then are we to regard the stem if it has not the value of an independent morphological member? Although this theme is so delicate, and its treatment so difficult for those who are not initiated into the details of the speculative science of form, yet I will try to briefly state the grounds which have led to the opinion stated above

At the free extremity of a growing leafy shoot a slight difference may indeed be recognized between the cells of the periphery and those of the interior, but no clear boundary can be fixed between these parts, and the end looks like an undifferentiated conical or hemispherical mass of tissue. On observing more narrowly the growth and further development of the mass, it will be noticed that cushions or protuberances arise on the periphery of the cone and form leaves, while the inner portion above these leaf-rudiments continues to elongate as an undifferentiated mass. Soon, however, fresh rudiments of leaves arise from it, and so as the process continues quite a large number of the cells are grouped together and form in their turn the starting-points of leaves. If we examine the tissue of a leaf as it arises thus below the tip of the shoot, we shall seek in vain for the place where the substance of the leaf ceases and that of the stem begins. It is on such grounds as these that the view has been formulated that the whole stem is really nothing else than a collection of leaves, standing one above the other, whose basal portions remain united, while the peripheral parts according to need rise up and project more or less. Against this view, of course, there is apparently the fact that not only leaves but also lateral shoots appear on the circumference of a growing shoot, from which it follows that the whole of the tissue is not employed in the formation of leaves, but that a part remains over from which the commencements of lateral stems are produced, and that it is this part which does not form leaves which represents the tissue of the main stem. It has also been proved that the rudiments of leaves arise on the growing shoot-cone from cells lying nearer the periphery than those from which the rudiments of lateral stems develop. This different origin has

been used as a mark for distinguishing between leaf and stem, and the peripheral tissue has been explained as the basis of the leaves, and the tissue lying below it as that of the stem-structures. The outer layer of cells of the growing cone, called *dermatogen*, never forms the starting-point for lateral stems, although it may occasionally give rise to leaves. The two or three outer layers of cells of the tissue below, called the *periblem*, usually form the leaves, but lateral stems often originate from the second to the fourth layers of the periblem. However, these possible differences of origin are insignificant, and no sharp limit can be drawn between the tissues from which originate the rudiments of leaves and lateral stems; consequently in this particular point there is no essential difference between leaf and stem.

In the stem the vascular bundles form a ring round the axis, but in the leaf-stalk, in other respects often very like the stem, they are grouped in a semicircle or in a plane. This, however, does not invariably occur. Leaf-stalks which bear peltate blades, as well as those which pass into blades with pinnate or palmate strands, as, for example, those of *Solanum jasminoides, Anamirta Cocculus, Menispermum Carolinianum* and of many other Menispermaceæ exhibit circles of vascular bundles and an actual ring of wood, so that they cannot in their internal structure be distinguished from stems. All other differences between leaf and stem which have been brought forward at different times and by different investigators apply indeed to a number, often to a very great number of plants, but unfortunately not to all. The following have been suggested as relatively the best marks of distinction, viz. that the leaf shows a limited growth, and that no new leaves spring directly from it, while the stem grows indefinitely and produces leaves laterally below its growing point. I say expressly the *relatively* best marks of distinction, because structures exist which cannot be forced into the limits of this definition. The flower-bearing as well as the flowerless phylloclades of the Smilacineæ (which are really reduced axes) have always a limited growth; and, on the other hand, there are plants from whose leaves other leaves grow out. In the leaf-blades of the American twining plant *Aristolochia Sipho*, which is often met with in gardens as a covering for arbours and trellis-work, green projecting bands and lobes, which can indeed only be explained as leaf-structures, sometimes arise on the lower side of the blade, especially in those places where the finer strands form delicate anastomoses. This is a case where leaf-like structures actually spring directly from leaves, and the only difference is that the places of origin of the leaflets are not arranged in geometrical succession.

On reviewing the results of the developmental and morphological researches, here only briefly touched upon, we are forced to confess that it is very difficult to state absolute distinctions between leaf and stem, and that, moreover, the view already mentioned, viz. that the stem does not form an independent member of the plant, is not really contradicted. The single fact opposed to this view is the occurrence of stems without leaves; those, for example, which spring from the seeds of *Cuscuta*. But here also it may be objected that this stem in its further development forms small leaves below the growing-point, and that its tissue is nothing more

than the continuation of the basal portion of these leaves. As in so many similar instances, the whole matter finally ends in an unfruitful strife of words where everyone is in the right. The simplest way is to regard as a stem every axis of a plant which, when developed, always bears geometrically-arranged leaves, and to avoid speculations as to whether this stem is to be considered as an independent structure apart from leaves, or as a combination of their basal portions.

Whatever theory we may hold of these relations, not only the form but also the function of the leaves borne by the part of the stem in question must be regarded as the predominating factor in the portrayal of the stem structure—especially when the peculiar construction of a given stem is to be explained by the special duties assigned to it.

There is no plant in which the stem is developed quite uniformly from the base to the apex. We can always distinguish in it stories following one above the other, each of which is fashioned in accordance with the work it has to perform. Just as in buildings the underground walls, which serve as the foundation of the whole and usually also as a store-room for food, &c., exhibit quite a different kind of structure from the upper stories which are inhabited, and where kitchen, bed-rooms, airy parlours and passages are found, so, in one and the same plant, different plans of construction are realized according as to whether the part in question bears cotyledons, scale-leaves, foliage-leaves, or floral-leaves, the functions of which are so extremely various. It therefore seems most natural to classify stems as hypocotyls, scale-leaf stems, foliage-stems, and floral-stems.

There is not much to be said about the *hypocotyl* (*fundamentum*). The little that is of interest has been stated already in describing the cotyledons. After it has drawn the cotyledons from their envelope and has straightened itself, the hypocotyl undergoes no alterations worth mentioning and is only of importance in that the bud of the main shoot is developed from its apex, and the food absorbed by the radicle is conducted by its means to this bud.

The stem bearing scale-leaves (*subex*) is usually so short in its first stages that its leaves lie close packed above one another, the upper ones being wholly or for the most part covered by the lower. In many instances it remains very short throughout life, and is then termed a reduced axis or "short branch". In others it extends and elongates so that its leaves are separated, and it is then called a "long branch". It may happen that one of these scaly stems is at intervals sometimes a long and sometimes a reduced axis; it may then be compared to a string, in which knots have been tied at certain distances. In the case of a scaly stem passing over into a foliage-stem beset with green leaves, the former usually has the form of a reduced axis. It is then either flattened or disc-like, or it may be of a shortly cylindrical or conical form. If it is beset with large scale-leaves and is considerably thicker than the leafy foliage-stem into which it almost directly passes, we speak of it as an abbreviated stem. This, together with its large and hollowed scale-leaves, is termed a *bulb* (*bulbus*); it is almost always underground, and its axis is vertical, as, for example, in lilies, tulips, hyacinths, and stars of Bethlehem.

A scale-leaf stem which remains short, which is clothed with membraneous scales and does not exceed in thickness the foliage or floral stem which often proceeds from it, is called a *sucker* (*surculus*). The sucker, beset with scale-leaves, appears as a bud (*gemma*) so long as the foliage or floral stem has not grown out from it; later it forms to some extent the basis of the foliage or floral stem, and is not very remarkable, especially after its hollowed scale-leaves, as is almost always the case, become detached and fall off. The scaly stem is but seldom developed at the base of the first shoot (plumule) arising between the cotyledons (*e.g.* in the Moschatel, *Adoxa Moschatellina*). On the other hand, it is scarcely ever absent from the base of the lateral shoots of woody plants, those bearing leaves as well as those which are terminated by flowers. In the subterranean buds of undershrubs the stem is occasionally very thick, and such buds have almost the appearance of bulbs. The subterranean buds, especially those of shrubs and trees, always possess, on the other hand, a short cylindrical or conical stem.

The *tuber* (*tuber*) seems to be to some extent a link between the reduced and the long axes formed by scale-leaf stems. It is always thicker than the shoots arising from it; its scale-leaves are situated so far apart that a clear space is visible between them, and they never cover and envelop one another. The scale-leaves of the tuber are insignificant; they only appear as narrow horizontal bands, or they are merely indicated by ridges and protuberances. In old tubers the scale-leaves are often scarcely recognizable externally. Most tubers are, moreover, very perishable structures; all those which appear as local thickenings of an underground shoot, of which the Potato (*Solanum tuberosum*) may serve as a type, grow very quickly, and have a resting-period of about half a year, but perish completely after they have developed shoots from their buds (the so-called "eyes") which unfold their green foliage above ground in the sunlight. Perennial tubers, whose lower half only is often embedded in the earth, or which are only covered with a thin layer of soil, are much less common. From these spring up every year a few shoots which, however, do not completely exhaust the tuber, but, on the contrary, supply it with materials manufactured by the green foliage in the sunlight, by which means the tissue of the tuber is actually enlarged. These perennial tubers frequently look like tuberous leafy stems, and the whole history of development must be known in order to be able to determine and prove that they really are scaly stems. Tubers are generally subterranean. More rarely they are formed above the soil in the axils of foliage-leaves, as, for example, in the Lesser Celandine (*Ranunculus Ficaria*), where those remarkable little tubers arise, which become detached after the withering of the plant; they afterwards lie on the ground, and have often, where they have been produced in great quantities, given rise to the myth of "potato rain".

Whilst some of the stems which bear scale-leaves are green, others are devoid of chlorophyll, and of these latter the following types may be distinguished:—first, the aërial, thread-like, twining and parasitic stems of the genus *Cuscuta*; second, the thin subterranean shoots of the Couch-grass (*Triticum repens*) and of numerous

allied grasses, clothed with sheathing, membraneous scales; third, the erect and fleshy stems of the Balanophoreæ and Orobanchaceæ, covered with dry scales (*cf.* figs. 41 and 42); fourth, the branched stems of *Lathræa*, lying embedded in the earth, covered with large fleshy scales (*cf.* fig. 37); fifth, the coral-like scaly stems branching in all directions, which have no roots and are only covered with delicate scale-leaves, as shown by *Epipogium* (*cf.* p. 111) and by the Coral-root (*Corallorhiza innata*); sixth, the stems of the Tooth-cress (*Dentaria*), creeping underground with thick, fleshy scale-leaves and clearly defined roots; seventh and last, the cylindrical, subterranean stems with weak membraneous scale-leaves and many roots, as in Solomon's Seal (*Convallaria Polygonatum*), the Sweet Spurge (*Euphorbia dulcis*), and numerous other perennial undershrubs. Subterranean scale-leaf stems developed as elongated shoots are classed together in botanical terminology under the name "root-stock" or "rhizome" (*rhizoma*); the term "creeping stem" (*soboles*) is applied to the thin, branching scaly stems which often creep for a considerable distance under the ground.

In the forms belonging to the first, third, fourth, and fifth groups, just enumerated, the scaly stem passes directly into a floral stem, *i.e.* on the same stem below are to be seen scale-leaves which stand in no direct connection with the processes of fertilization, and above them perianth leaves, as in the Rafflesiaceæ (*cf.* figs. 44 and 45), or bracts, as in the Broom-rape and Toothwort (*cf.* fig. 37). In these plants no green foliage leaves are developed; they are unnecessary, because these plants are all parasites or saprophytes, and do not require to manufacture organic compounds for themselves, but derive the material necessary for their further growth from their host, or from the humus of the forest ground. In plants of the other groups, of which *Dentaria*, Couch-grass, and Solomon's Seal may be taken as types, two kinds of shoots are developed:—Shoots whose stem is beset only with scale-leaves without chlorophyll, and those which branch off from these grow up above the ground, and there unfold green foliage-leaves. Here, too, must be mentioned those strange plants whose perennial underground stems develop two kinds of shoots which appear above ground;—first, shoots whose stem is covered below with scale-leaves, but which bears flowers above and later on when these first shoots begin to wither, leafly, flowerless shoots whose green leaf-blades unfold in the sunlight. This remarkable division of labour is observed in many Alpine plants, in species of Butter-bur (*Petasites*), and in the widely-distributed and well-known Colt's-foot (*Tussilago Farfara*).

Green scaly stems which develop as elongated shoots are obviously all aërial, or rather, they grow above the ground and the cortex of their stems becomes green so far as the light can influence them. That part of the shoot which remains hidden in the dark earth does not become green, and many such shoots, *e.g.* those of *Asparagus*, are white and without chlorophyll in the lower half, their upper portions alone being green, viz. the small needle-shaped branches (phyllocladia) growing out from the axils of the small scale-leaves. Amongst the green scale-leaf stems must be included the cactiform plants, the switch plants, and the plants with

flattened shoots, which have been fully described on p. 333. The Horsetails (Equisetaceæ) belong also to this group, and in one group of these (*Equisetum arvense*, *E. Telmateja*) the division of labour is similar to that in the Colt's-foot. The first pale shoots which emerge from the ground are terminated by a spike of sporangia-bearing scales, and not until later, after the spores have been scattered by the wind and the pale primary shoots have withered, do the summer shoots appear whose stems develop green tissue in the cortex.

The inner structure of the green scaly stems, whose duty is to manufacture organic materials, agrees essentially with that of the foliage-stem. In these plants, indeed, the functions have only been transposed in this way, viz. that normal green leaves are not produced, but only small colourless scales, whilst the work usually allotted to the leaves has been assumed by the cortex. Green scaly stems are just as much exposed to wind and sunlight as leafy stems are; they must, like them, direct and establish themselves in accordance with the particular conditions of their habitat and offer the same resistance to the wind; they must be just as elastic and flexible, and consequently present a similar arrangement of their tissues rendering it possible for them to maintain the favourable position once assumed. The subterranean scaly stems have no need of such contrivances; no winds press against them and their tissue does not require to be strengthened against bending. The stems of Balanophoreæ require only a slight elasticity, the part which rises above the ground is relatively very thick and almost reminds one of the stalks of the cap-fungi. Many of these scale-leaf stems under the ground or rising only a little above it, are very brittle, and when stems of *Dentaria*, embedded in the humus of the forest soil, are dug up, the greatest care must be taken to prevent their breaking. The same is true of underground tubers and bulbs; they need none of those contrivances by means of which a definite position with regard to the light, or a great capacity of resistance to wind is obtained. Protective measures against excessive transpiration are likewise unnecessary, and this accounts for the lack of cuticle to the epidermal cells, and for the absence of hair-like structures and varnish-like coatings. When dry, tough scales occur as envelopes to bulbs, they are probably of a protective nature—not against transpiration or over-illumination, but against subterranean animals which might come and nibble them for their food-reserves.

These subterranean shoots excavate their own bed by the pressure which their turgescent tissues exert on the surrounding earth during growth. Growing bulbs and tubers in this way widen out a bed, often of considerable size, and the pressure exerted is so great that the loose earth in their neighbourhood becomes compressed, and sometimes transformed into hard cakes. It has already been mentioned that not only stiff soil but even bits of wood and other objects may be bored through by the stiff, pointed scale-leaves of the Couch-grass. A most important function falling to the lot of underground shoots, and especially to tubers and bulbs, is the storage of reserve materials. These are manufactured during the summer by the green tissues in the sunlight above ground and are then conducted down into the

subterranean reservoirs. Here they remain quietly deposited during the winter and are not brought into requisition until the plant, at the beginning of the next vegetative period, sends up new shoots which manufacture organic materials afresh. It is in the production of these shoots which are to be sunned above the ground that material is always employed which was conducted down into the storehouses during the preceding year.

We cannot help surmising that this remarkable alternation between rest and vigorous activity, together with the temporary disappearance of all the aërial portions of the plant, is connected with the peculiar conditions of the habitat. This opinion is confirmed by the actual distribution of tuberous and bulbous plants. Most of these plants are found in those regions where all the succulent tissues exposed to the air would be liable to the danger of shrivelling up in consequence of months of drought, and where also the superficial layers of soil in which the tubers and bulbs are embedded dry up so much that they would not be able to replace the water evaporated from the leaves. But when the soil has lost all its water, it forms an excellent protection to the tubers and bulbs; the earth forms an actual crust round the succulent structure, and in many regions the clay soil, coloured red by iron oxide, is hardened into a mass which resembles brick. Embedded in this mass the tubers and bulbs can survive the dry period which lasts over seven or eight months with impunity. When the rainy season comes and the hard crust is moistened, a wonderful life stirs everywhere through it. Innumerable tuberous and bulbous plants spring from the softened clay and unfold their flowers and green foliage-leaves during the brief wet period. This is what occurs in the clay steppes of Central Asia, in the mountainous districts of Asia Minor, in Greece, and generally all the countries bordering the Mediterranean Sea. In especial degree is the Cape celebrated for its almost inexhaustible wealth of bulbous and tuberous plants ("cape bulbs"). In Central Europe, where the activity of vegetation is interrupted not by dryness but by frost, the number of these plants is strikingly less than in the districts previously enumerated, whilst the ground in which the few species occur exhibits quite different conditions. Here the soil is never exposed to severe drought, indeed, strangely enough, the majority of tuberous and bulbous plants in the depths of the Central European forests are found in loose and dampish earth, rich in humus. It is well known that in such places as these snowdrops and yellow *Gagea*, the Two-leaved Squill, the purple Martagon Lily, the Cuckoo-pint, the Broad-leaved Garlic, and the various species of Corydalis (*Galanthus nivalis*, *Gagea lutea* and *G. minima*, *Scilla bifolia*, *Lilium martagon*, *Arum maculatum*, *Allium ursinum*, *Corydalis fabacea*, *C. solida*, *C. cava*), flaunt themselves with a luxuriant and vigorous growth; and, what is especially worth noticing, their flowers blossom in the first part of the year, their green foliage unfolds early in spring and at midsummer is already yellow and withered, although, as stated, the necessary moisture would not be lacking at this season.

This peculiar phenomenon demands a reason, and we shall not be far wrong if we explain the preference of our early-flowering bulbous and tuberous plants for

the ground of forests somewhat as follows. The leaf-covered forest floor, sheltered as it is by the trees, gives out but little heat, and the frost only penetrates it to a slight depth in the winter, thus the tubers and bulbs are far less exposed to the danger of freezing than in the open country. The early flowering and the quick fading of the leaves are caused by the fact that the light required for the activity of the green foliage can only penetrate to the forest ground while the crowns of the trees are bare. Later, when a leafy canopy and shady roof is spread out above, only a sunbeam here and there can steal through the chinks to reach the damp, cool soil of the forest ground. But this scanty light would no longer suffice for the work to be done by the green leaves of the bulbous plants, and they must therefore achieve this before the leafly roof has developed. The weak light is, however, quite sufficient for parasites and saprophytes, and it is worthy of notice that in the summer in place of the green leaves of bulbous and tuberous plants, which even in June have turned yellow and disappeared, the *Monotropa* without chlorophyll, the leafless *Epipogium*, and a host of pale fungi spring up from the deep humus in the gloom of the forest.

STEMS BEARING FOLIAGE-LEAVES.

The foliage-stem (*stirps*[1]) is characterized by the fact that the leaves borne upon it are provided with green blades, and realize the popular idea of leaves. This portion of the stem might indeed be called "foliage-leaf stem", and its essential characteristic would be expressed in the term, but since the cotyledons frequently assume the form of foliage-leaves, it is perhaps better, in order to avoid confusion, to keep to the term "foliage-stem". No part of the plant is so striking to the eye as the foliage-stem. The rhizomes, tubers, bulbs, and other forms of scale-bearing stems are hidden from view in the earth, just like roots. The flowers borne by the floral stems are ephemeral structures, the leafy stems alone retain their character during the whole vegetative period as the most important portion of the plant. When one attempts to reproduce the character of the vegetation of any region either in words or in the form of a picture, it is to the leafy portions of grasses, shrubs and trees that one confines oneself; these, blended in infinite variety, compose the carpet of the meadow, the bush, the thicket, the woods and forests. It is the style of architecture of the foliage-stem, so to speak, which expresses the style of the whole plant-body.

This peculiar style of architecture, and the habit of the whole plant subservient to it, depends primarily upon the size, length and thickness of the foliage-stem. It is evident that in this respect conditions obtain quite analogous to those in the

[1] Agreement in matters of terminology is only partial among botanists. The older botanists used the term *stirps* as synonymous with "plant" (*planta*); later it was claimed for the *stem* in the wider sense. The entire main axis of flowering plants was called the "*caudex*" by Linnæus, and from it he distinguished the descending portion or root (*radix*), and the ascending part or stem (*stirps*). In modern times the term *caudex* has been employed in a different sense from that of the Linnæan terminology for the stems of palms. Here the stem of a plant is spoken of as the *cormus*, it is divided into: (1) The hypocotyl (*fundamentum*); (2) the scale-leaf stem (*subex*); (3) the foliage-stem (*stirps*); (4) the floral stem (*thalamus*).

already-described scaly stems; here only are the differences in size more marked. Contrasts, like that between filamentous leafy stems, barely a centimetre long, and the giant trees of North America and Australia, have not their like in the whole vegetable kingdom. In those plants which germinate, grow, blossom, and fruit and, after the distribution of their seeds, perish, all in a single year—in these short-lived annuals—the foliage-stem seldom attains to a considerable diameter. In many small Cruciferæ, *e.g.* in the small-flowered Shepherd's Purse (*Capsella pauciflora*) and in the tiny Chaffweed (*Centunculus minimus*), the diameter of the stem often scarcely amounts to half a millimetre. The largest dimensions in annuals are found

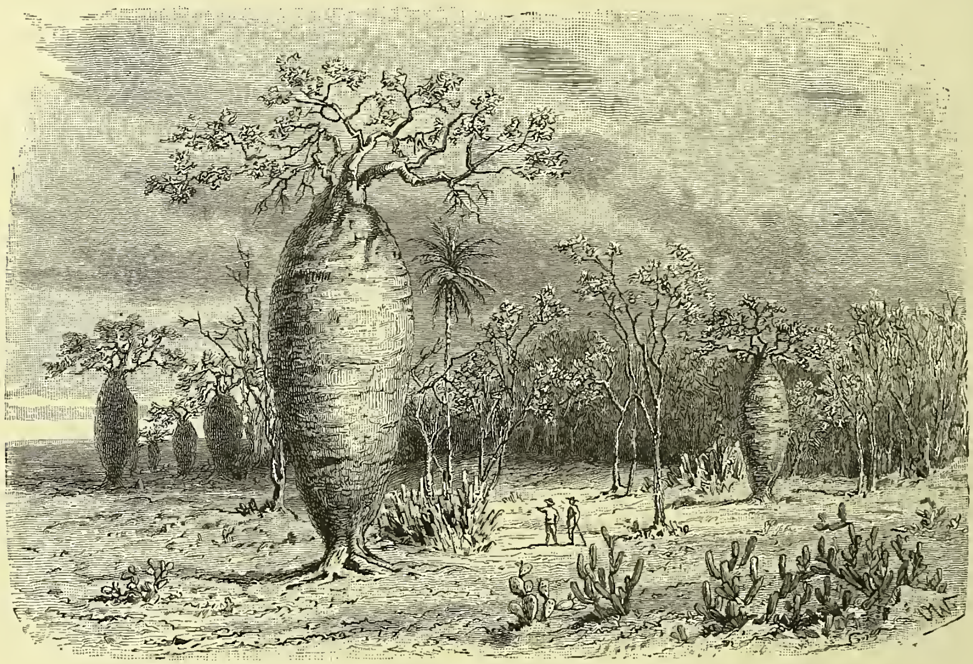

Fig. 152.—Cotton Trees (*Cavanillesia tuberculata*) of the Brazilian catingas. (After Martius.)

in the Castor-oil plant (*Ricinus communis*), many of the stems attaining to a diameter of 7 centimetres, and in the balsams of the Himalayas (*Impatiens tricornis* and *glanduligera*) which sometimes have a diameter of 4 centimetres. In these annual plants the stem which bears the leaves perishes with them every year. It is otherwise with plants whose stem remains alive for more than one period of vegetation, and which have been called perennial. When these throw off their foliage, they do not die, but fashioning themselves into supports for the leafy shoots which arise from their buds, attain a circumference in just proportion to the new burden to be borne. The structure of such foliage-stems then becomes altered. The stems of annuals and those of the young new shoots of perennial plants have a green succulent cortex with a peculiarly-developed epidermis; such a shoot we call "herbaceous" (*stirps herbacea*). In the leafless stems of perennial plants, now transformed into columns, a dried crust or bark replaces the succulent green cortex

whilst within masses of wood are continually formed and are deposited on the bundles of woody cells and vessels produced in the first year—thus increasing the circumference of the stem. Such a stem is said to be "woody" (*stirps lignea*). Woody stems which have been thickened continuously in this manner for centuries sometimes attain a circumference of 50 metres; that of the Mexican conifer

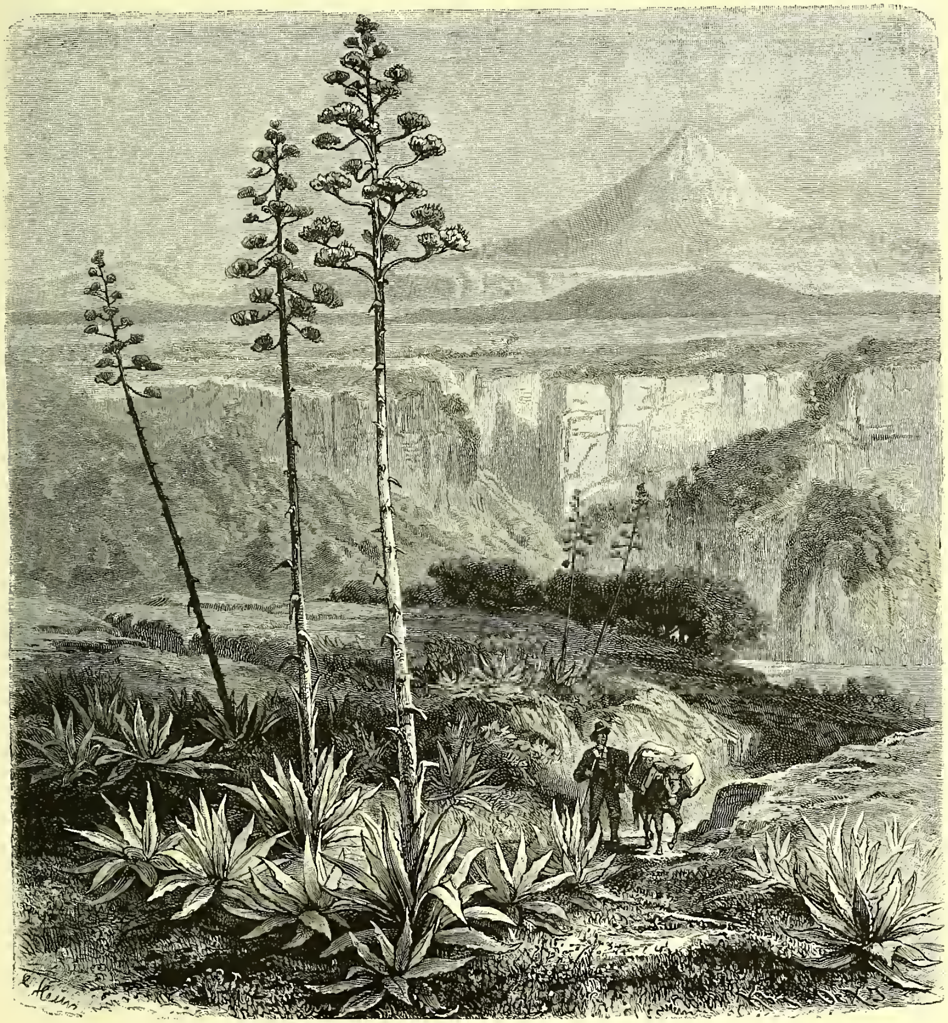

Fig. 153.—Agaves of the Mexican uplands (from a photograph).

(*Taxodium mucronatum*) has even been found with a girth of 51·88 metres; this circumference exceeds that of the above-mentioned stem of *Centunculus* more than a hundred thousand times. The thickness of the stem is in general greatest at the base and gradually tapers off above; only a few palms are thicker immediately below their crown of green leaves than at the base, and in the strange cotton-trees of the Brazilian catingas (*Cavanillesia tuberculata*) of which an illustration is inserted opposite, the stem forms a swollen, barrel-shaped mass attaining its maxi-

mum about half-way up. Very often an unequal thickening may be observed in the foliage-stem; this is due to the fact that at the places where leaves arise from the stem knotty swellings are developed, while those portions of the stem which come between successive leaf-insertions (or nodes), and which are called *internodes*, are cylindrical or prismatic in form. A foliage-stem which has this peculiarity is said to be "nodose" (*nodosus*). Sometimes the internodes of such nodose stems adjoin one another at obtuse angles, and such a stem is then called in botanical terminology "zigzag" (*flexuosus*).

The fully-developed internodes of which the foliage-stem is built up, are only rarely, and then only for short distances, of precisely equal length. Sometimes longer and shorter internodes alternate, and quite as often it happens that a single much-elongated internode succeeds several short ones. If such an elongated internode passes over into the region of the flowers, it is known as a "scape" (*scapus*). As in the scaly stems, where short and long axes can be distinguished, so is it with the foliage-stem. The leaves are usually so crowded on these short axes that they form rosettes or fascicles which quite cover the stem which bears them. On the other hand, on many long axes the leaves are developed scantily and at long intervals and we are tempted at first glance to take such an elongated shoot for the leafless stem of a switch-plant. A large number of plants develop in one year only short axes with rosette-like radical foliage-leaves; in the following year the apex of the short axis grows up into a slender, elongated shoot which passes above into a floral stem. This is the case in most plants whose stem is said to be "biennial" (*stirps biennis*). Similar conditions are observed, however, in many perennial species of house-leek (*Sempervivum*), *Aloe*, and various other plants with fleshy, succulent leaves, only in these the alternation of long and short axes extends over several, often very many years. A very noticeable form of this kind is *Agave Americana*, known by the name of the "Century Plant", illustrated in fig. 153. Often 20, 30, even, it is alleged, 100 years pass by, during which long period the plant produces only a short stumpy axis beset with leaves grouped in a rosette. At length a long axis arises from the centre of the rosette and terminates in a voluminous inflorescence. As soon as the fruits have been produced from the flowers, and the seeds have escaped, not only the long axis, as in biennial plants, but also the short axis with its large, stiff and spiny rosette-leaves entirely dies away. In water-plants this type is also met with in the remarkable Water Soldier (*Stratiotes aloides*), to which allusion has been so frequently made. In this plant, as in the house-leeks and saxifrages, long axes which continue to grow until they have arrived beyond the circle of the whole rosette, arise from the axils of the lower leaves; when this has happened, the young horizontally-projecting shoot stops extending, and at its tip again forms a short axis, *i.e.* a rosette, which, in the following year, sends up a fresh long axis. A similar alternation of long and short axes is also observable in numerous other plants, in the shrubby spiræas, and in roses, hawthorn, sea-buckthorn, barberry, and *Astragalus*, which we shall encounter later on as hedge-forming shrubs. Some-

times long and sometimes short axes develop from the same shoot. Also in many conifers, *e.g.* cedars and larches, the branches proceeding from a shoot are for the most part short with needle-like leaves arranged in fascicles, and only a few of

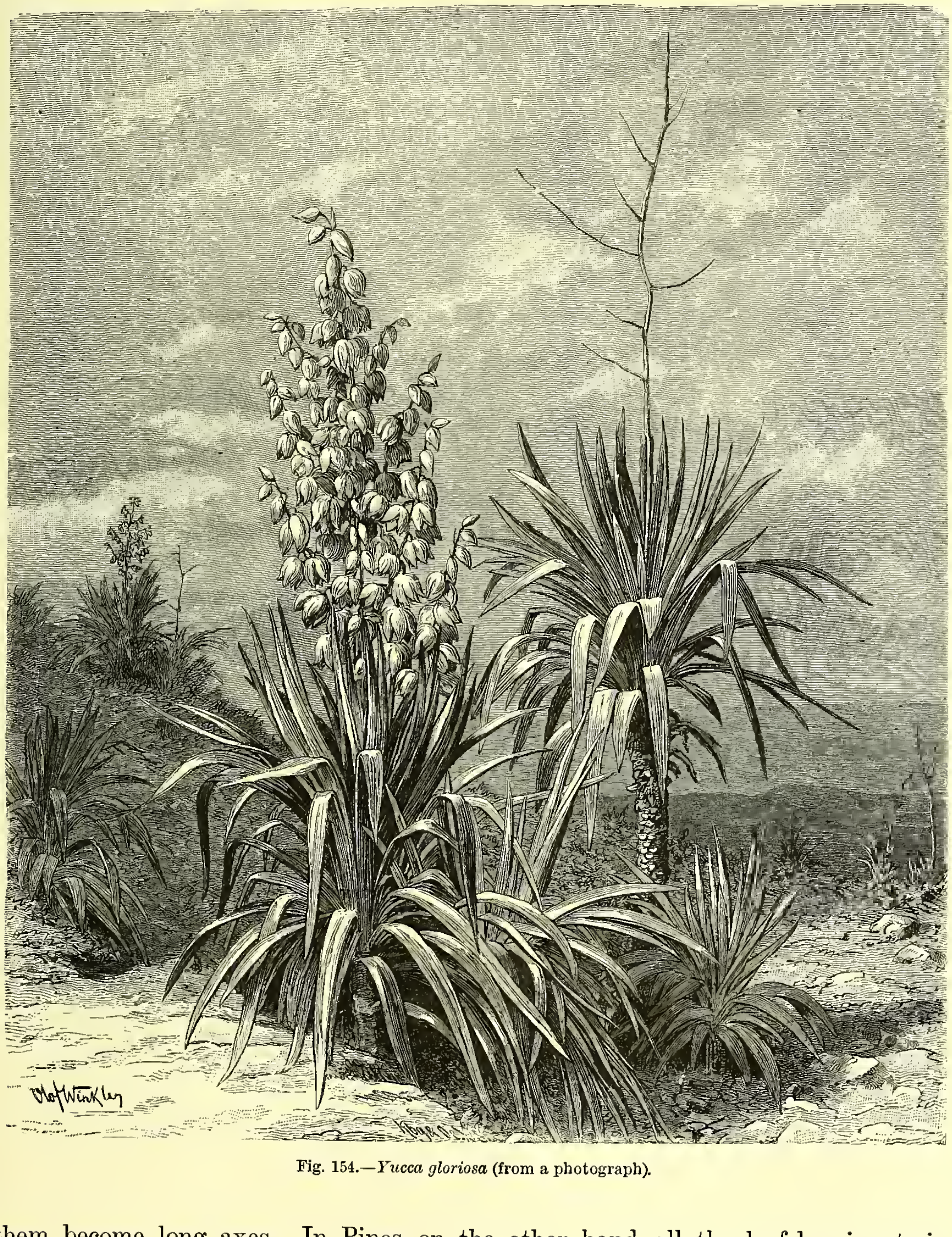

Fig. 154.—*Yucca gloriosa* (from a photograph).

them become long axes. In Pines, on the other hand, all the leaf-bearing twigs are short axes, and here we have also the remarkable circumstance that in several species, *e.g.* the Scotch Pine (*Pinus sylvestris*) a lateral twig bears only two such needle-leaves. Tree-ferns, Cycads, Pandaneæ, Grass-trees (*Xanthorrhœa*), many

palms, dracænas, and species of Yucca, of which the *Yucca gloriosa*, illustrated in fig. 154, may serve as a type, exhibit a very peculiar structure. The yearly increase in length of the stem is comparatively small, the leaves which project all round from this portion of the stem are consequently crowded together and form a rosette which cannot be distinguished as regards the arrangement of the individual parts from the radical rosettes of Agaves and species of house-leek, and, like these, must be regarded as a short axis. In the following year the stem continues this curious, abbreviated growth, the foliage-leaves of the previous year gradually die off, and only the hardened remnants of their leaf-bases are left behind, thus the rosette or head of fresh green leaves is now seen borne by a naked columnar stem. This continues for many years, and the gigantic crown of leaves rises higher and higher above the ground. Plants with this manner of growth, moreover, never attain even in many years to anything like the height which is attained by foliage-stems terminating in or branching out into long axes. Even the tallest palm terminating in a short axis is a dwarf in comparison with the rotangs or climbing palms, continually shooting out long axes. Rotang stems are known to extend to almost 200 metres. The length of 200 metres is perhaps the extreme limit reached by a foliage-stem, and if we again contrast the extreme cases, and compare with these climbing palms the stems of the minute *Gentiana nana* growing on the high Alps, it is seen that the shortest known of all foliage-stems is exceeded by the longest about twenty thousand times, in round numbers.

The ramification and facies of foliage-stems is in main part governed by the light-requirement of the leaves they bear. Necessarily the foliage-stem as the bearer of organs which have to prepare organic materials in the sunlight is chiefly influenced in its growth, and as to the position which its branches assume by the conditions of illumination. In order that all the green leaf-blades of a plant may be suitably illuminated, it is necessary that all these foliar axes should be grouped conformably, and should divide up the space most economically. Where foliage is chiefly borne on short branches, even under the most favourable conditions, only a relatively circumscribed space can be utilized. But when the reverse is the case and foliage is produced on long branches, the plant is much more favourably circumstanced. Such plants can unfold their leaves gradually above one another, and display them at appropriate intervals and distances to the sunlight. This elevation of the leafage above the ground is rendered possible either by the possession of a specially-contrived stem, or through the employment by the stem of some strong substratum or support up which it climbs to the light. Again, long axes, which have not the capacity of rising above the ground in either of these ways can elongate while embedded in the soil or extended on it, and, running out in all directions, can arrange their green leaves in a mosaic-like carpet. Lastly the foliage-stems can be sustained in the position most suitable to their leaves by means of the surrounding water. According to the circumstances, foliage-stems may be broadly classed in four groups, viz. those which lie on the ground (*stirpes procumbentes*), those which float in water (*stirpes fluctuantes*),

those which climb (*stirpes scandentes*), and the erect columnar stems (*stirpes palares*).

PROCUMBENT AND FLOATING STEMS.

If we review the plants whose characteristic appearance is chiefly due to their procumbent foliage-stem, we notice that most of them take root in turf, boggy ground, on the stony plateaus of hilly districts, in the rocky clefts of wind-swept mountain heights, or, lastly, in the sandy plains of the lowlands; in general they inhabit an infertile soil, on which the storm has free play, and where erect plants would find it difficult to maintain themselves. The leaves of such stems are usually undivided and small, and are present in large numbers on each year's growth. Where their number is small, and where correspondingly the internodes of the annual shoot are more elongated, the leaves are often divided, but then the individual segments are of the shape exhibited by the leaves of the short-membered shoots. The leaves always appear in two or three rows on the fully-formed procumbent stem, whether they are decussate or spirally arranged (*cf.* p. 417). Where no local insurmountable obstacles exist, the procumbent stems spread out in all directions from the spot where the plant first took root, and when the species in question are sociable weave a close carpet over the ground in a relatively short time. In the earliest stages of development the shoots are not extended over the ground, that is to say, the primary shoots, originating directly above the hypocotyl, are at first erect. Soon, however, as it elongates, the stem inclines to one side and nestles to the ground, or it arches over so that its free end reaches the soil. The apex of course is always more or less erect, and most young, procumbent shoots have the shape of an ∽. As the stem elongates, the part immediately behind the growing-point always nestles to the ground. In many instances these stems have not the strength to hold themselves erect; the soil on which they lie is their actual bed or support. If stems like these are held up above the ground, they hang limply down, as may be seen in the Periwinkle (*Vinca*), Strawberry (*Fragaria*), and in the Japanese Saxifrage (*Saxifraga sarmentosa*) so often grown in hanging baskets. But in all cases it is not their weight merely which causes many shoots to assume this manner of growth, in other words, that the shoots do not sink to the ground under the burden of their leaves, can be seen plainly enough in the procumbent stems of hawkweeds which produce runners (*e.g. Hieracium Pilosella*); these, when gathered and placed upright, remain quite stiff and straight, and do not show the slightest bending. When the stems of *Globularia cordifolia* or those of the Hairy Genista (*Genista pilosa*), growing on a rocky ledge, reach over the edge, they do not hang down vertically, as would be the case if their own weight were exclusively the cause of the direction taken, but they skirt along the face of the overhanging rock and remain closely pressed against it.

The first group of plants with procumbent foliage-stems is perennial; the growing-points of their stems advance over the substratum a little every year, and the new-formed shoot is the continuation of the older portion of the already

existing stem. At first the new portion of the stem is directed upwards, but after a year it lies flat on the ground or is actually pressed to it. It then sends out lateral branches which repeat the method of growth just described, but it always remains fresh and vigorous, serving for years after it has thrown off its leaves for the conduction of food from the ground and only dies off very gradually and slowly from behind.

In many forms belonging to this first group the older portions of the stem become lignified, and persist for a very long time. They may also increase in thickness, exhibiting numerous annual rings, as, for example, the stems of procumbent willows clinging to the rock terraces of the high Alps, as illustrated on p. 524. The elongating stems do not often throw out additional roots, as may easily be shown by raising the stems from their procumbent position. When such stems branch, and the branches have spread far and wide over the soil, they form an actual carpet, which can be raised from the ground or from the rock terrace as a coherent mass, as, for example, in the red Bearberry (*Arctostaphylos Uva ursi*) and the white Dryas (*Dryas octopetala*). Many members of this group possess evergreen foliage, as we see in the Trailing Azalea (*Azalea procumbens*) and *Globularia cordifolia*. The Cinquefoils with trailing woody stems (*e.g. Potentilla nitida* and *Clusiana*), Sibbaldia (*Sibbaldia procumbens*) and several valerians (*e.g. Valeriana tripteris* and *montana*), similarly provided, possess, however, no evergreen foliage, and may be distinguished from those named earlier by the fact that the annual increase of their stems is very slight, in consequence of which the older plants have usually a turf-like appearance. Many species of Thyme (*Thymus*) are, on the contrary, characterized by the fact that they every year develop fairly long and thin whip-like shoots which weave over the mossy substratum, or, like Dryas, form a carpet on the rocky bed. The stem of the forms hitherto brought forward is termed "prostrate" (*stirps prostrata*), from which is distinguished the "creeping" stem (*stirps repens*). Even when it has lost its leaves, the creeping stem is not lignified, but develops abundant root-fibres close behind the growing-point, which penetrate into the ground, and often draw the stem down into the soil or mud. The growths of former years do not here persist so long as in plants with woody prostrate stems; they usually die off after three or four years, and decay and vanish away altogether. Thus one might almost imagine the stem had been shifted *en masse*, that it had crept forward in the direction of the growing tip. Sometimes on the older portions of these stems, the situations where leaves were formerly inserted are marked by transverse scars and bands—reminding one very much of creeping worms and caterpillars. The umber stems of the Californian *Saxifraga peltata* which creep over damp rocks by the sides of streams are very striking in this respect. A likeness to worms crawling over the soil is also possessed by the stems of the European and American Asarabacca (*Asarum Europæum* and *Canadense*), by those of the marsh-inhabiting Buckbean (*Menyanthes trifoliata*), of the Snake-root (*Calla palustris*), of the purple Marsh Cinquefoil (*Comarum palustre*), and of several species of clover (*e.g. Trifolium repens* and *fragiferum*).

In addition and in contrast to this first group of plants with procumbent foliage-stems there is a second, characterized by the fact that only the buds arising on the new shoots remain throughout the year, strike root, and grow out into new plants, while the shoots themselves—the axes from which the buds have been developed—soon perish, thus severing the connection with the parent plant. These shoots are always thin, frequently quite thread-like. Little building-material is wasted upon them, since they are but ephemeral structures. Two distinct types of stem may be distinguished in this second group. These are known as the stolon and runner. By "stolon" (*stolo*) we understand a procumbent stem which dies off after a year, and is abundantly beset with leaves not very far apart. In the axils of many of these leaves no buds are produced, and often only at the ends of the stolons do buds arise from the axils of very minute leaves; these buds take root. This is especially the case in the arched stolons, as, for example, in the well-known Periwinkle (*Vinca*), and the purple Gromwell (*Lithospermum purpureo-cœruleum*). The shoots arising from old plants of these species form flat arches abundantly beset with pairs of leaves. Their free ends lie on the ground, swell and grow down into some dark chink or into the black humus itself, striking root and thus being drawn still deeper into the ground. The end of the stolon, thus embedded, finds itself next year, so to speak, on its own feet; it grows up into a new plant, while the arched or connecting portion dies off sooner or later, and in the following year, or the year after that, vanishes, leaving no trace. The stolons of the Pennywort (*Lysimachia Nummularia*) are similarly constructed, but in this plant the shoots lie flat on the soil, and the tip does not thicken, nor do the apices avoid the light, or become drawn far into the earth. Rooting buds arise in the axils of small leaves close to the up-bent apex of the stolon, and in the following year become starting-points for new plants. Several species of saxifrage and house-leek (*Saxifraga* and *Sempervivum*), the Common Bugle (*Ajuga repens*), some hawkweeds (*e.g. Hieracium Pilosella* and *Auricula*), and numerous other plants develop richly-leaved stolons which produce at their free ends short axes which root. The leaves on these short axes are grouped in rosettes; the short axes grow next year into new plants, the intervening stolon perishing. A peculiar modification of this method of growth is found in certain house-leeks (*Sempervivum arenarium* and *Soboliferum*). Here, as before, the tip of the thread-like stolon develops a short axis with leaves arranged in rosettes, but as soon as this is fully formed, the stolon withers, the spherical rosette becomes detached from it and rolls down over the steep ground where it had developed. Since these species of house-leek grow as a rule on the narrow ledges of precipitous rock-faces, it happens that the rosette thus detached falls from ledge to ledge, often to a depth of many metres, truly a remarkable method of distribution, which we shall allude to again in the second volume (cf. vol. II. fig. 425).

The "runner" (*sarmentum*) is distinguished from the stolon by the fact that its internodes are much elongated, and that leaves and buds which strike root and form the starting-points of new plants, are only formed at wide intervals

on them. The long bare internodes are always thin and thread-like, and perish in the course of a year. One portion of the buds developing at the nodes of the runner forms short axes; another part may form even in the first year long axes which again assume the form of a runner. Since each plant sends out simultaneously several runners extended on the ground on every side, it comes to pass that in a very short time considerable areas are spun over in all directions with filamentous runners and a host of new plants produced. Well-known examples of this form of procumbent stem are furnished by the strawberries (*e.g. Fragaria vesca, grandiflora, Indica*), several cinquefoils (*e.g. Potentilla reptans* and *Anserina*), the Creeping Avens (*Geum reptans*), the Stone Blackberry (*Rubus saxatilis*), the Ground Ivy (*Glechoma hederacea*), and the Japanese Saxifrage (*Saxifraga sarmentosa*). A very peculiar appearance is presented by *Androsace sarmentosa*, which grows in the Himalayas. All its leaves are crowded together into a beautiful rosette on an erect short axis. From the axils of several of these rosette-leaves, long, thin runners, red in colour, radiate out during the summer; they extend themselves on the rocky soil, and each runner forms at its end only a single rooting bud or rosette. The red filaments perish in the second year, but by this time five or six freshly-rooted rosettes may generally be seen standing in a circle round the older one.

In a third group of plants the whole procumbent foliage-stem with all its branches dies off every year at the close of the vegetative period. The plants belonging to this group are either annuals and maintain themselves only by seeds, or they possess perennial subterranean scaly stems, in which case each year new leafy stems arise. The foliage-stem of these plants is said to be "prostrate" (*stirps humifusa*). The following may serve as examples of such annual, prostrate shoots: — The Caltrops (*Tribulus*), the Strapwort (*Corrigiola*), *Illecebrum*, the Pimpernel (*Anagallis*), the Ivy-leaved Speedwell (*Veronica hederifolia*), the Portulaca (*Portulaca oleracea*), and numerous species of Polygonum, trefoil, and medick (*Polygonum, Trifolium, Medicago*); as examples of perennial prostrate plants — the Bird's-foot Trefoil (*Lotus corniculatus*), the variegated Coronilla (*Coronilla varia*), and several caryophyllaceous plants (*e.g. Saponaria ocymoides, Telephium Imperati*).

When the leafy shoot lies on the soil, it can easily dispense with the development of those cells which would otherwise be required to give to its stem strength for support and resistance to bending. Thus plants with procumbent stems have an advantage in this respect over such as stand erect, in that they can economize so much building material. On the other hand, however, the procumbent form has the disadvantage of being able to expose to the light relatively little green tissue; only those of its leaves can be well illumined which are arranged like a mosaic in a plane parallel to the substratum. The development of a second such layer of leaves higher up would be a decided disadvantage, for it would cause the lower stratum of foliage-leaves to turn yellow and pine away. Consequently, any upward extension of the green tissues in procumbent shoots is

necessarily limited. Again, the earth offers an insuperable barrier to the development of foliage in a downward direction. In the dark bosom of the earth a green leaf would be quite useless, and, as a matter of fact, there is not a single plant whose green tissue is situated in the depths of the soil.

With water it is otherwise. In it green cells and tissues can function as far down as the light can penetrate. Since the water also maintains the stem and leaves in a definite position, and the plants consequently are spared the development of wood and bast and, generally, of masses of tissue for strength and resistance to bending, and since, finally, a saving of material and work is effected inasmuch as water-plants do not require to construct organs for conduction of water and for transpiration, it might be supposed that water would be an extremely favourable medium for green vegetation, and that, consequently, stretches of water all over the world would be quite crowded with green plants. That this is not the case is explained by the fact that light does not penetrate far enough into the water. In the deep gloom, 200 metres below the surface, green plant-life is as impossible in water as in the dark bosom of the earth, and the bottom of the ocean over an enormous area is a plantless waste shrouded in gloom. But as far as the water is illuminated, in all places where it fills shallow basins, and also in a comparatively narrow girdle around the coasts, an inexhaustible wealth of plants is to be found. Of course, spore-bearing plants, which are built up of rows, nets, and plates of cells, have the preponderance, whilst seed-plants are markedly in abeyance in relative number of species. But the latter species are just the ones which claim our interest in a special degree on account of the very peculiar conditions under which they live.

The *floating* stems of water and marsh plants, as already repeatedly stated, have no wood or bast, while, on the other hand, they are penetrated by remarkably large air-canals, and are, in consequence, exceedingly light and buoyant. If the erect stem of a water-plant growing at the bottom of a lake is cut through close above its roots, it rises immediately to the surface of the water, there assumes a horizontal position, and remains floating; under certain circumstances it may continue to grow and may perhaps take root should it drift to a shallow place. On the other hand, if a pond filled with Water Crowfoot, *Myriophyllum*, *Elodea*, &c., be emptied, all these plants sink limp and withered on to the mud, as their stems have not the strength to hold themselves erect. The water in which they float supports and bears them, and in this respect they may be likened to climbing stems which also require a support to enable them to rise above the ground. The analogy between these plants is evident in so far as the need for "more light" influences the direction of growth in both cases—in the one case the stem grows out from the gloom of the forest floor up to the sunny tops of the trees, in the other, from the subdued light at the bottom of the lake up to the surface of the water. In many cases, of course, the stem of water-plants remains so short that it scarcely rises above the mud at the bottom of the pond, but the leaves arising from it are shaped into long ribbons, whose

freely floating ends ascend into the better illuminated upper layers of water, or leaves with large blades and elongated stalks spring from the short stems, and the stalks continue to grow until the plate-like blades have reached the surface, where, floating, they can enjoy the full sunlight. There are also some plants not fixed but swimming close to the surface. These sink down to the bottom only when the activity of their leaves is suspended and here for a time they pass a dormant period.

We mention here the most noticeable variations which are made use of for dividing the stem-forming water-plants into architectural groups. First of all is a group of plants, of which the Grass Wracks (*Zostera*) may be taken as a type. These have stems embedded in the mud, creeping, and anchored by root fibres. The leaves arising from these stems are erect, very long and narrow, looking like thin limp ribbons, which are only kept in their erect position by the water. The *Zostera* grows in large patches on the shore between tide-levels. Its leaves are collected and dried and under the name of Sea-grass are used as stuffing for cushions. To this group belongs also *Vallisneria spiralis*, which is figured opposite, and to the flowers of which we shall return in detail later on; lastly, we may mention certain species of *Sparganium*. In addition to this group is a second, as a representative of which may be named the curious Lattice-leaf plant (*Aponogeton fenestrale* or *Ouvirandra fenestralis*) inhabiting the waters of Madagascar. Its short stems are buried in the mud; the leaves have short stalks, and are not erect, but distributed in rosettes over the muddy bottom. The green colour of their chlorophyll is almost entirely obscured by a reddish-brown pigment; the parenchyma, which usually fills the meshes of the net-work of strands, is absent, and the strands forming the framework of the leaf-blade are covered only with a thin layer of chlorophyll-bearing cells, so that the whole structure reminds one of a leaf which has fallen from a tree in autumn and has been macerated under water, of which, after the falling away of the easily decomposed parenchyma, only the net-work of strands remains. The Water-lilies may serve for a type of the third group. Their stems are short, rooted in the mud, and send out leaves whose broad blades, often circular in outline, are borne on very long stalks. The disc-shaped leaf-blades lie with their under side on the surface of the water, while their upper surface is exposed to the air. The leaf-stalks thus traverse the whole depth of the water, and look like ropes by which the floating leaf-discs are anchored in the muddy bottom. The long scapes, terminating in floating flowers, serve a similar purpose. Here also must be included the aquatic fern-like plant—*Marsilea*. Its leaves remind one of those of the Wood Sorrel. The Frog-bit (*Hydrocharis*) and the Villarsia (*Limnanthemum*) form a fourth group, not unlike water-lilies on a small scale. Their leaves and flowers, however, do not arise directly from the main stem (as in the last group), but from long lateral shoots, quite bare of leaves, till just close to the surface (*cf.* vol. II., fig. 419). Our fifth group includes forms transitional between the groups already described and the sixth and largest group. They include forms with

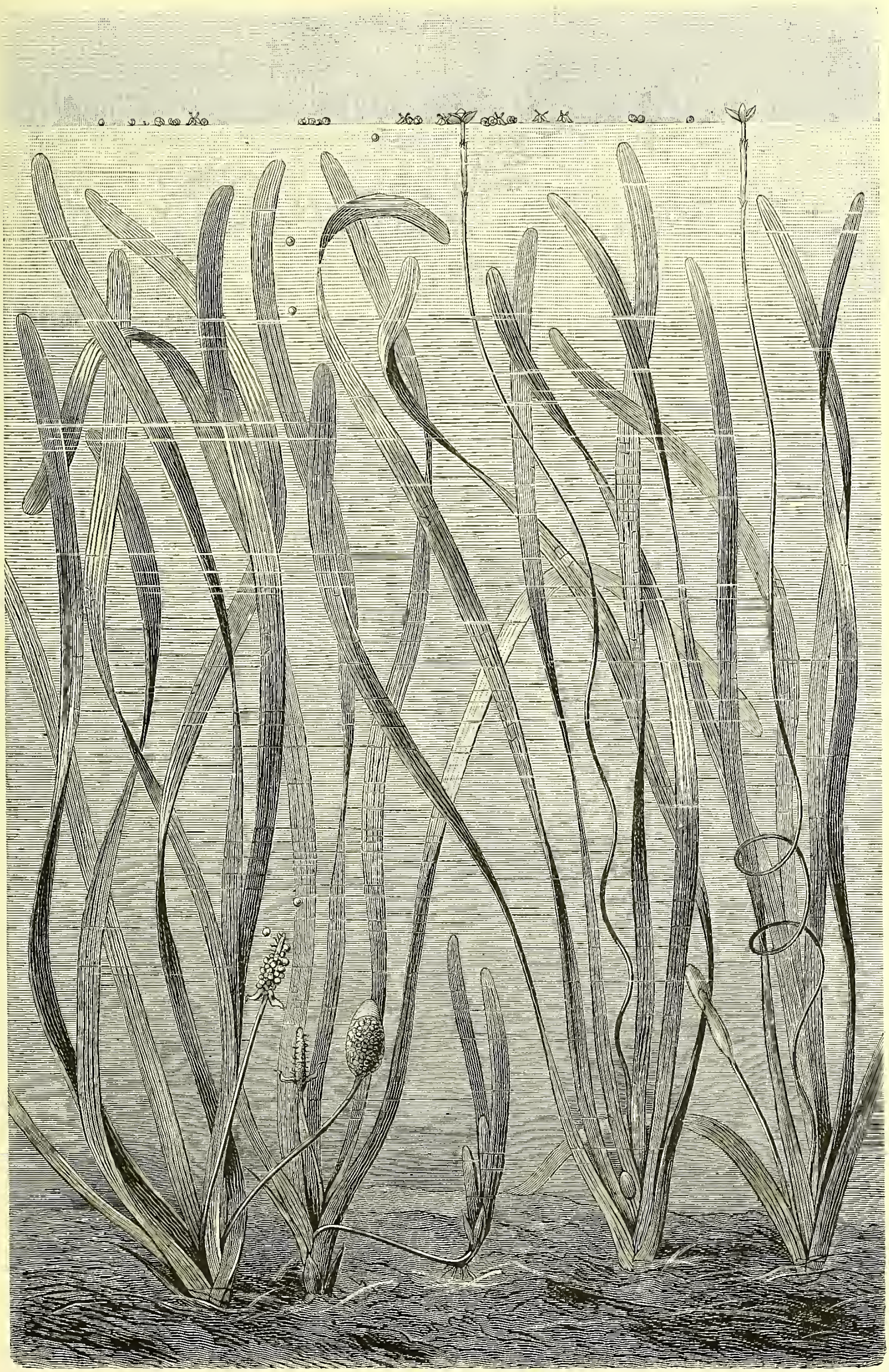

Fig. 155.—*Vallisneria spiralis.*

finely-divided, submerged leaves, in addition to orbicular floating ones as in the water-lilies, &c. Such plants are known as heterophyllous (*plantæ heterophyllæ*). Examples are furnished by several potamogetons (*Potamogeton heterophyllus, rufescens, spathulatus*), some water-crowfoots (*Ranunculus aquatilis, Baudotii, hololeucus*), the Cabomba (*Cabomba aquatica*) and the Water-chestnut (*Trapa*). In the sixth group the plants are firmly rooted in the mud like those of the former group, but the shoots rising from them bear only submerged, thin and limp leaves. These plants in descriptive botany are called "submerged" (*plantæ submersæ*). Their leaves — arising from the much-branched filamentous stems — exhibit an endless variety of form. They are sometimes decussate, sometimes spirally arranged, often broad and embracing the stem, and then again fall into the opposite extreme, and form long very narrow ribbons or threads. Frequently they are reduced to mere bristles; in other cases they are entire and undivided; again, in other instances, they have finely indented and sinuous margins (*cf.* fig. 136, p. 551). All these various forms of leaf are connected with the peculiarities of the habitat, with the attacks of animals to which they are liable, with the conditions of illumination at different depths of water, but chiefly with the direction of the foliage-stem. The long thin stems can only maintain a vertical position in still water, and only in the calm inlets of lakes and in the deep pools where an active movement of the water is impossible are to be found species whose submerged leaves, arranged at definite intervals, exhibit a circular form. In running water, especially in quickly-flowing streams, the leaves are always long drawn out, ribbon-shaped, filamentous, or divided into thread-like lobes. They adapt themselves exactly to the current, and follow it in all its movements uninjured. These leaves of running water are always fairly tough; their cell-walls are correspondingly thickened; the stems from which they arise are protected against rupture by bundles of bast deposited in the cortex, and are strengthened against strains by various other contrivances to be presently described.

While the foliage stems of the water and marsh plants hitherto described are anchored fast by roots to the muddy bottoms of lakes, pools, and streams, those of the *Aldrovandia*, figured on p. 151, and also of the bladder-worts described and figured on pp. 120, 121, float in the water without a trace of root formation. Since the leaves require light, it is clear that they will take up their position near the surface. At any rate at the time when they are actively engaged in the manufacture of organic matter under the influence of light, they are obliged to seek such illuminated places. The bud-like tips of the shoots can, of course, in many species sink to the bottom for the winter rest, but at the commencement of the favourable season next spring, they again ascend and produce their flowering axes above the surface of the water. A horizontal, or obliquely ascending position is the most advantageous for the stems of these floating plants as regards the illumination of their leaves, and, as a matter of fact, this direction is observed in them. Running water would form a bad environment for such rootless, freely oscillating plants; they are found exclusively in the calm inlets of ponds and lakes and in pools and

ditches amid reeds and rushes, where a great agitation of the water has never to be provided against.

In similar habitats other species of the last group of plants with floating stems are also found, viz. those known as "swimming" plants (*plantæ natantes*). They are distinguished from floating plants especially by the fact that their green foliage and in part their stems also lie on the surface of the water, and are in contact on the upper side with the air, or even rise above the water, when they are completely surrounded by air. The stem rests and moves on the surface of the water, and is never held fast in the muddy bottom—even when roots are present. Amongst the well-known forms belonging to this group are several Duckweeds (*e.g. Lemna polyrrhiza, gibba, minor*) with stems curiously flattened and leaf-like. Besides these, there are *Salvinia* and *Azolla*, belonging to the vascular cryptogams, and finally several species of *Pistia*, *Pontederia*, and *Desmanthus*, belonging to tropical waters. It has already been mentioned (p. 638) that the floating capacity of *Pontederia crassipes* is increased by the possession of a vesicular, air-containing tissue in its swollen leaf-stalks. Moreover, in *Desmanthus natans* an actual swimming apparatus is developed, not in the leaf-stalks, but in the stem itself. It takes the form of a large-celled, spongy, air-containing mantle, arising here below the epidermis of the internodes which renders sinking impossible. The mimosa-like foliage-leaves rise up from the nodes of these floating stems like masts with flags. When the leaves turn yellow, the stems rid themselves of their swimming organs which are no longer needed, and indeed it appears to be an advantage to the leafless stems to be able to sink down and to obtain a period of rest at the bottom.

Several species of the last group of plants with floating stems strongly remind us of plants with procumbent stems. At the stem-nodes they develop roots which sink into the depths, and green leaves which rise up to the sunlight, and the only difference consists in the fact that in the one case the water, and in the other the soil, forms the bed, and even this distinction is sometimes obliterated. When the level of the water sinks, the floating plants sink with it, till finally they lie on the mud, and then, as a matter of fact, they are scarcely distinguishable in habit from plants with procumbent stems which grow on the soil of the moor.

CLIMBING STEMS.

Often it happens that the name of a plant affects our imagination by its pleasing or harmonious sound. One associates with the name not merely the idea of the form of a certain plant, but more than this, its whole surroundings, framed in which it grows and flourishes. One conjures up a picture of a flowery meadow or scented wood with which the plant with pleasing name can only harmonize. It may be some far-back reminiscence is bound up with the pretty name, or we have read a vivid description in a book long ago. Thus idealized, one shrinks from approaching it with critical eye, from examining it with knife and microscope, and from classifying and describing it in the dry language of the specialist.

I am thinking here especially of the word "*liane*". When this beautiful word is sounded a whole series of splendid pictures stand out in strong relief from the twilight of youthful recollections. I see a dense leafy canopy, lit by a stray sunbeam here and there, arching over the gigantic stems of the primeval forest—stems which rise up like the columns of a spacious hall. On the forest floor the scanty green of shade-loving ferns covers the remains of fallen trees. Further on a confused brown mass of tangled roots renders progress over the still dark ground almost impossible. In contrast to these gloomy depths how brilliant is the picture in the glades and on the margin of the primeval forest! Plant forms in indescribable confusion piled up into the thickest of hedges rise higher and higher to the very crowns of the giant-trees, so that it is impossible to obtain even a glimpse into the pillared hall of the interior of the forest. This is the true and proper home of the liane. Everything climbs, winds, and twines with everything else, and the eye in vain attempts to ascertain which stems, which foliage, which flowers and fruits, belong to which. Here the lianes weave and work green draperies and carpets in front of the stems of the forest border, there they appear as swaying garlands, or hanging down as ample curtains from the branches of the trees. In other places they stretch in luxuriant festoons from bough to bough and from tree to tree, forming suspension bridges, even actual arcades with pointed and rounded arches. Isolated tree-trunks are transformed into emerald pillars by the covering of woven lianes, or more frequently become the centres of green pyramids over the summit of which the crown spreads out in verdant plumes. Where the lianes have grown old with the trees on which they cling, and the older portions of their stems have been long stripped of foliage, they resemble ropes stretched between the ground and the tree-summits, and often assume peculiar and characteristic forms. Sometimes drawn out tightly, sometimes limp and swaying, they rise up from the undergrowth of the forest ground, and become entangled and lost far above among the boughs. Many are twisted like the strands of a cable, others are wound like a corkscrew; and others again are flattened like ribbons, hollowed in pits, or shaped into elegant steps—the celebrated monkey-ladders.

The green garlands, bowers, and festoons of lianes are adorned with the gayest flowers. Here a truss glows with flame-like brilliancy, there a large blue raceme sways in the sunshine, and here again is a dusky curtain studded with hundreds of bright star-like passion-flowers. And where flowers flaunt themselves and fruits ripen, guests are not wanting. The gay assemblage of butterflies and the joyous songsters of the wood regard the forest border interwoven with lianes as their favourite rendezvous.

From what has been hitherto said about lianes, one might think that this particular plant formation belonged only to the tropics. This would, however, be incorrect. In the neighbourhood of the Canadian lakes, and in the districts of the large central European rivers, the Danube and the Rhine, various species of Clematis, wild vines, climbing roses, honeysuckle, bramble, many Menispermaceæ, &c., climb up to the summits of the trees; and even the woods of our lower Alps contain one

of the most charming lianes, the Alpine Vine (*Atragene alpina*), adorned with large, blue, bell-shaped flowers. Of course the number of species increases immensely as we approach the torrid zone, and we shall not be far wrong if we estimate the number of lianes in the tropics at 2000, those in the temperate zones at 200 species. Lianes are foreign to the Arctic regions and to the treeless mountain heights; nor are they found on treeless steppes. It is remarkable that tropical America contains almost twice as many climbing plants as tropical Asia. Brazil and the Antilles exhibit the greatest wealth of these plants.

The sweet word "liane" originated in the French Antilles, and has now found its way into most languages. It seems strange that this word should never have been introduced into botanical terminology; we use the expression indeed in general descriptions of the vegetation of a district, but in that of individual species it is avoided. This is explained by the fact that we understand by lianes in the original sense of the word only climbing plants with woody perennial stems, and that there are many twining, creeping, and climbing plants possessing herbaceous stems to which the name liane is not properly applicable. On the other hand, the climbing plants are so much alike in their manner of life that they can only be treated together, and are therefore conveniently designated by a common name. We now name all inclusively "climbing plants", whether woody or herbaceous, and define the "climbing" stem (*stirps scandens*) as that which is able to obtain for its free end a resting position at a great height above the nourishing earth only by the aid of foreign supports. If, where climbing stems grow, there are no elevated objects which might serve for support, the earth itself is used by the free end as a resting-place; the stem then spreads its whole length upon the ground, or forms an arch, having at any rate its free end supported on the ground. Such a stem shows all the characteristics of a prostrate stem. In the earliest stages of its development, on the other hand, every climbing stem resembles an erect plant; it is difficult to name external characteristics by which young shoots of the one can be distinguished from those of the other. The shoots at first are erect and able to maintain themselves in a vertical position by their inner structure, and especially by the turgidity of certain groups of cells. Not until they have become older, and have reached a certain height does indication of a climbing habit appear, when the shoot seeks to obtain a hold for its free end. It curves over foreign bodies in the vicinity, thrusts out horizontal branches over projecting edges of rocks or in the forks of boughs of trees which serve as supports; its tip revolves like the hand of a watch, and winds round an erect post, or it develops special organs, by which it becomes connected and entwined with adjacent objects. In respect of their varying behaviour, climbing stems may be divided into five groups, viz. weaving, lattice-forming, twining, creeping, and climbing, of which classification, of course, as in so many similar cases, it must be noted, that it is purely artificial, and is only used with the object of distinctness, and that intermediate and transitional forms between the several groups occur in abundance.

The *weaving* stem (*stirps plectens*) obtains a resting-place for its branches and

foliage in the following manner:—As a young shoot it grows first of all vertically erect; it has as yet no lateral branches, and its leaves at the free-growing end are still small, furled, and crowded closely together into a cone. These young turgescent shoots readily pass through the forks of the boughs, even through narrow chinks and meshes of the net-work of twigs and branches in the thickets, without suffering injury. When its growth in length is terminated, the shoot unfolds its leaves and sends out lateral branches which project at right angles in all directions. These reflexed leaves and the lateral branches which have been produced above the gaps in the matted undergrowth, now get a good purchase on the rough boughs of the underwood; the slender upgrowing shoot is suspended by them as if by barbs, and it is frequently also actually woven into the underwood.

These forms of weaving stems may be distinguished according to the character of the support. First, that of the hedge-forming shrubs, of which *Lycium* may serve as type. It is astonishing how its long whip-like shoots, as they grow up from the ground on the edge of a wood, find their way between the spar-like branches of other growths, and then perhaps at the height of the lowest boughs of the crown of one of the trees, the free end projects as if from an opening in a roof. In the course of the summer the thin slender stem lignifies, and leafy lateral shoots spring from the axils of the upper leaves at about a right angle. These end in stiff spines. Meanwhile the highest portion of the shoot becomes bent over some bough, so that the whole shoot is so interwoven with the undergrowth, that in attempting to extricate it we tear innumerable supporting branches and twigs, and set the whole neighbourhood in motion. The lignified shoot of the first year survives the winter; next spring those portions of it which rest horizontally on the branches produce new shoots in pairs, close to the thorny lateral branches. Of these one usually remains small; the other, slender and vigorous, pushes up into the crown and repeats the method of growth of the former shoot. As this is repeated from year to year the whole crown of the tree becomes densely interwoven with the *Lycium* shoots. Often it happens that shoots are produced, which hang down from the tree-crown like branches of a weeping-willow draping the supporting tree as with a curtain, or forming an actual hedge in front of it.

The following well-known plants develop in accordance with this *Lycium* type:—Numerous roses (*Rosa*), brambles (*Rubus*), barberry (*Berberis*), spiræas (*Spiræa*), sea-buckthorn (*Hippophaë*), jessamine (*Jasminum*), *Celastrus scandens*, and numerous other woody hedge-formers which grow preferably on the borders of forests. Many roses, as, for example, the *Rosa sempervirens*, abundant in the Mediterranean floral district, not only weave through the undergrowth, but often reach the tops of the highest oaks. Also many brambles (*Rubus*) reach far up into the boughs of the tree-crown, and then not unfrequently depend their long shoots in arching curves. I measured the length of a stem, ½ centimetre thick in the middle, of a species of bramble (*Rubus amœnus*) which had interwoven with the tree-crown, and found it to be six and a half metres. The long whip-like shoots of *Jasminum nudiflorum* and *Celastrus scandens* also reach the tops of high trees

in the same manner. If these hedge-shrubs have not the opportunity of interweaving in the branches of trees, &c., they are obliged themselves to form a scaffolding. Their manner of growth resembles that already described, except that the shoots usually remain shorter, and the whole plant consequently appears more compressed. The erect shoots at first mounting vigorously upwards form, as they become lignified, flat arches, bent over so that their apices almost trail upon the ground. The upper portions of these arches give rise next year to short flowering branches and to long vigorous shoots, which give rise to new arches. The free ends of the old arches dry up, and fresh arches come to lie above the dried remains. In the following year new arch-like shoots proceed from the last-formed ones. This being repeated year after year, an impenetrable natural hedge gradually rises, which grows continually higher and higher, since the stumps of the old, dried-up branches, whose ends have stopped growing, form supports for the younger shoots. It is also a very common occurrence for these hedge-shrubs, when they have become old, to develop suckers from their roots, which grow up, thin and slender, between the undergrowth formed of the old, dried-up arches, which they use as a support. This may be seen especially in the barberry, sea-buckthorn, mock-orange, roses, jessamine and the elm-leaved spiræas.

This property of forming hedges has long been familiar to agriculturalists, who are close observers of nature. Several such plants are used for the purpose of inclosing portions of land; thorny species are especially suited for the purpose, the so-called "quickset hedges". Gardeners, too, make use of this peculiarity of hedge-weaving shrubs when they plant species with beautiful flowers close against a trellis-work, which is soon quite overgrown with their vigorous shoots. The so-called climbing-roses in particular are used with the best results for covering trellis-work against the fronts of buildings, and it is remarkable how quickly they grow without assistance right up to the gables of the houses. Some climbing roses (*e.g. Rosa setigera*) have this remarkable peculiarity, that their new shoots at first seek the darkest places, turning their apices away from the bright sunshine, growing into the shaded nooks behind the trellis-work, and not inclining again towards the light until they are fully grown. In this way the advantage is obtained that the shoots originally turning from the light enter the gaps of the undergrowth and of the trellis-work, while later on, when lateral branches arise from them, they are excellently supported.

Generally resembling the woody stems observed in hedge-builders are those of several undershrubs which do not become lignified. The shoot growing up annually at the beginning of the vegetative period from the underground portion of the stem always dies off again in the autumn, whilst the dried remains still above the ground decay so quickly that only in rare cases can they be used as supports for the shoots which grow up fresh from the soil in the following year. As a type of weaving undershrubs the widely-distributed Marsh Crane's-bill (*Geranium palustre*) may be taken. The young shoots grow erectly among the bushes scattered over damp meadows or on the edge of a forest, but they do not become woody; their upper ends

do not bend over the supporting branches, but, having once attained a certain height, develop stiff lateral branches, projecting like spars, and long-stalked leaves which push their way between the stiff, dry branches of the supporting bushes; in this way the whole shoot is held fast so that it cannot be displaced. When this same Crane's-bill grows in a meadow between low herbs which can afford it no support, the stem bends and the whole shoot lies with its lower internodes on the ground. The ends of the internodes are thickened, and a turgescent cell-tissue is formed at these places by means of which the younger parts of the shoot are brought again into an erect position, appearing at right angles to the older internodes lying on the ground. The advantage obtained by this arrangement, is that plants of Crane's-bill thus extended over the ground are able, should they encounter a firm shrubby undergrowth not too far removed from the place where they are rooted, to use it as a support and to weave themselves over it. As a matter of fact, plants of *Geranium palustre* are often seen with their lowest internodes lying on the ground, while the upper internodes as well as numerous lateral branches are interwoven into some bush growing in the meadow near by, and their red flowers are displayed more than a metre high above the soil from between the branches of the bush serving as a support. Several other species of crane's-bill resemble this one in habit (*e.g. Geranium nodosum, divaricatum,* &c.), also several species of bedstraw and woodruff (*e.g. Galium mollugo, Asperula aparine*), the berry-forming Cucubalus (*Cucubalus baccifer*), and, finally, the remarkable Marsh Speedwell (*Veronica scutellata*). Here, too, belong several species of asparagus with projecting, spar-like branches and filamentous or needle-shaped phylloclades. The annual shoots of these asparaguses attain an astonishing length and push their way into the forkings of the boughs of erect-growing stems. In this respect the *Asparagus acutifolius,* very common in the region of the Mediterranean flora, is particularly worth mentioning, and also the *Asparagus verticillatus* growing in Asia Minor, the stems of which not infrequently attain a length of 3 metres, climbing up to the crowns of the lower oaks and there interweaving their horizontally disposed branches with the boughs.

The third group of plants with weaving-stems includes the rotangs, those peculiar palms celebrated for the fabulous length of their almost uniformly thickened stems. A species of rotang, drawn from nature in Java by Selleny, is given on the opposite page. The stem of all young rotang plants is erect, and the yet folded leaves grow vertically upwards in the same direction as the young axis. Later, when the leaves unfold and expand, they arch outwards and spread themselves over the confused mass of other growths, amongst which the rotang plant has germinated and grown up. If the vegetation in the immediate neighbourhood consists only of low herbs and bushes, the elongating rotang stem does not find a support sufficient to enable it to grow up in the original vertical direction. So it trails on the ground like a runner, often forming snake-like coils, as shown in fig. 156; still always bending up at the free end, and continually pushing up new leaves. If the rotang plant has developed amongst tall shrubs and trees, or if after

Fig. 156.—Rotangs in Java. (From a drawing by Selleny.)

trailing, it has come within the range of a wood, it pushes its stiff, folded, spire-like leaves between the lower branches of the trees, and as these leaves unfold and bend outwards, they form strong supports or barbs by which the cord-like stem is anchored above in the branches of the tree (*cf.* fig. 94, p. 363). Under favourable conditions the stem can grow up to the tops of the trees, its new leaves always anchoring thus in the branches above. Frequently the free end of a rotang shoot

Fig. 157.—Shoot-apices of three species of Rotang.

1 *Dæmonorops hygrophilus.* 2 *Calamus extensus*; with inflorescence. 3 *Desmoncus polyacanthus*; much reduced.

grows from tree to tree—now ascending, now descending. It is shoots of this kind which attain to lengths unequalled by any other plant. There are credible statements according to which such rotang stems, with an almost uniform thickness of only 2–4 cm., have reached a length of 200 metres.

We must not omit to mention that most, if not all, plants which weave into the thicket of other plants are equipped with barbed spines, prickles, and bristles, which assist them in maintaining themselves at the heights once reached. The goat's thorn is provided with horizontally-projecting spines; in the roses and brambles

both the internodes and the ribs of the leaves are beset with sharp, backwardly-directed prickles; several bedstraws (*e.g. Galium uliginosum* and *aparine*) bear short, stiff, reversed bristles on the ridges of the stem and on the leaf-margins and ribs, whilst the midrib of the pinnate rotang leaves is continued beyond the blade as a long whip-like structure beset with barbs of the most varied description. The illustration of three species of rotangs inserted opposite shows the most striking forms of these peculiar leaves. In one species (fig. 157 [1]) the leaf-rachis is beset at equal intervals with groups of small but very pointed barbs; in a second species (fig. 157 [2]) the uppermost leaves are wholly devoid of green pinnæ, and bear only numerous claw-like barbs; while in the third (fig. 157 [3]), very long, pointed, reversed spines are found on the foremost portion of the leaf, with little teeth between, so that this

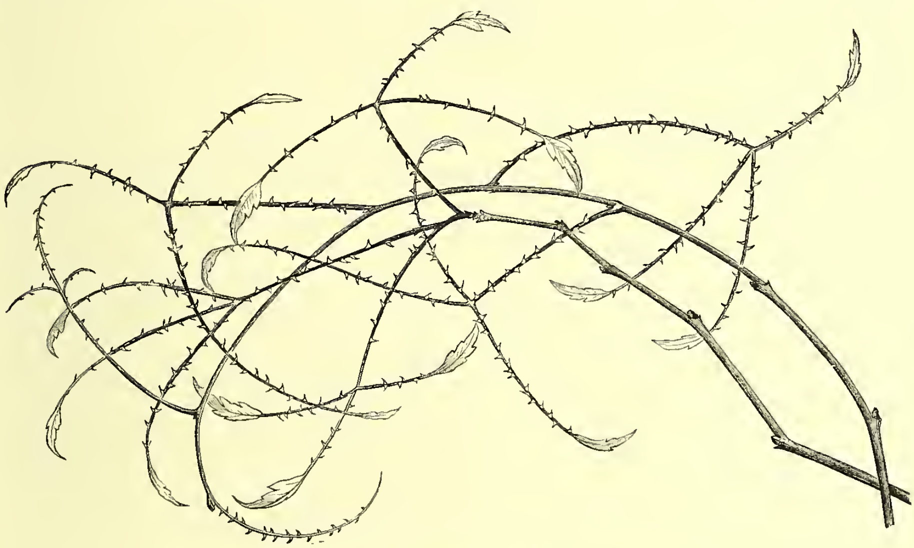

Fig. 158.—Branches of the New Zealand Bramble (*Rubus squarrosus*).

portion resembles a harpoon. When we look at these barbed structures and consider that the rotang leaves are exceedingly rough, we can understand how firmly the rotangs anchor themselves in the crowns of the tree-summits, and how difficult it must be to disentangle these climbers, fastened as they are with harpoons, from the trees they interweave.

A plant distinguished by its unusually rich development of barb-like spines, and deserving especial mention here, is the New Zealand bramble, *Rubus squarrosus*, illustrated in fig. 158. Each of its leaves is divided into three portions, each being provided with a tiny blade at its apex; these three portions as well as the leaf-stalk are green throughout their entire length and beset with yellow, pointed prickles which anchor so firmly in the intertwined bushes and shrubs that a wholly inextricable tangle is the result. Finally those plants still remain to be considered in which the support is afforded by the pointed teeth of the leaf-margin. To these belong especially several tropical Pandanaceæ, with long thin stems resembling rotangs,

and also an insignificant little speedwell which grows in damp meadows in Great Britain, and rises above the ground by sprawling over its erect and stronger neighbours. This speedwell (*Veronica scutellata*) has long, narrow leaves which in section almost resemble those of the tropical *Pandanus*. Like these they are erect when young, and are inserted in pairs over the vertically-growing apex. By the further growth of the stem they are pushed in between the gaps in the confusion of herbage. By and by the leaves are reflexed and afford the plant useful support. While the serrated teeth of the leaf-margins in other species of speedwell have their apexes directed forwards, in this they are strangely directed backwards, *i.e.* downwards towards the ground; by this means the support which these leaves obtain is materially increased. In this speedwell the retro-serrate teeth of the leaf-margin have undoubtedly no other significance than that of firm anchorage, though, in many of the other above-named instances, the pointed teeth, prickles, and spines have the additional task of protecting the foliage, and perhaps also the flowers and fruit, against animals which might climb up over the stem in their search for food.

The *lattice-forming stem* (*stirps clathrans*) does not twine, nor indeed has it any special climbing organs, and yet leaning against rock-faces or tree-trunks it gradually attains to heights which it would be unable to reach without these supports. It clothes its supports with branches, which, in the aggregate, constitute a solid lattice-work, reminding one of certain interweaving climbers, from which, however, it is distinguished by the fact that its elevation is achieved neither by lateral branches projecting like spars, nor by arched shoots, nor even by reflexed foliage-leaves. Lattice-forming stems occur comparatively seldom in the floras of the temperate zones; the most striking example in these regions is the small and dainty species of buckthorn known as *Rhamnus pumila*, whose lattice-work clothes the steep limestone rocks here and there in the outlying Alps between Switzerland and Styria, and in the Jura. Anyone looking from a little distance at a precipitous rocky face overgrown with this buckthorn, might think that it was ivy which had spread out its stems, climbing by means of clinging roots. The foliage shows, indeed, the same dark green and is about the same size as that of ivy, but it is easily recognized on a nearer view that the shape of the leaf, the distribution of the strands in the blade, and finally the character of the flowers and fruits are quite different, and, what is especially important here, that the much-branched woody stems adhering to the steep rocks have no clinging roots. It is also an interesting fact that the older stems are actually wedged into the crevices of the rock, and that the branches are exceeding brittle. With careless handling they break and fall to the ground, and only by proceeding very carefully can one succeed in detaching a complete stem with all its branches from the rocky face. We may conclude that this plant would necessarily perish without the supporting background, since its brittle branches would break off at the first violent burst of storm, and the bush would be mutilated by every tempest.

The peculiar structure and method of growth of this buckthorn explain all these striking phenonema. Here there are no strands of hard and fibrous bast deposited

outside the soft bast, such as enable the young branches of other trees to resist flexion or to resume their position after bending by the wind. In the centre of the branch is seen a woody cylinder, surrounded by strands of soft bast; and beyond this a very voluminous parenchyma, but only a very few hard tenacious bast-fibres. It is evident, therefore, why the branches break away so readily. And that they split up most easily at their places of origin, *i.e.* where they arise from an older branch, is explained by the fact that the woody cylinder is weakest at these points. The method of growth of the branch is just as remarkable as its structure. When in the spring leafy shoots proceed from the foliage-buds, they do not grow towards the light, as in the greater number of plants, especially woody plants, but they turn away from the light and seek the darkness, and even curve round projecting angles into shady corners, growing into the dark crevices and clefts in the stone wall. If the face is not cracked for a wide distance, but is smooth and even, the longer, growing shoots always hug it closely, and take a straight course; but, as soon as a fissure is reached, the shoot immediately bends round into it, much in the manner characteristic of roots (*cf.* p. 88). While in other shrubs the young, growing shoots arising from an old woody branch are directed upwards, it here frequently happens that a downward course is followed. The burden of the foliage unfolding on the shoots, and the consequent increase of weight cannot be regarded as the cause of this bending, for not infrequently from one and the same branch, as it runs horizontally over the rock wall, shoots arise side by side of similar shape, similarly leaved, and of about equal weight, some of which grow downwards and others upwards.

In this manner of growth it is unavoidable that the branches should sometimes cross one another, forming a lattice-work which adheres to the rock. I have never observed actual fusions of the intersecting branches in this buckthorn, but it often happens that the younger branches which lie across the older are so firmly attached to them that they still remain connected when large portions of the plant are removed from the rocky wall.

Such extensive lattice-branches have quite the appearance of a root-plexus which has extended over a boulder, and we are reminded of the remarkable latticed root-formation of certain tropical fig-trees, which will be discussed later on. There is also a temptation to take the older stems of *Rhamnus pumila* for roots, inasmuch as they are frequently seen embedded in the clefts and crevices of rocks, a phenomenon brought about in the following way. When the apex of the developing, light-avoiding shoot reaches a dark cleft, it continues to grow in a manner readily intelligible in the direction of the crevice, into which it nestles so far as its foliage permits. Later on it becomes lignified and loses its foliage; in the following year it sends up new shoots, but itself remains growing in diameter by the addition of wood and bast, till sooner or later it becomes so thick that it is jammed tight in the cleft, and resembles a root which has forced its way in.

The lattice formation in tropical Clusiaceæ, of which an illustration is given on page 681, is effected in a manner quite different from that obtaining in the buckthorn. The young stems of Clusiaceæ grow erect, and prefer to make use of

tree-trunks as supports, particularly those of palms. At first they adhere very slightly, and lean on them only to a certain extent. All the shoots of these Clusiaceæ are thick and beset with opposite leathery leaves; they remain green for a very long time, and are still unlignified when they develop lateral shoots from the leaf-axils of their erect branches, and when the cortex is wounded, a thick adhesive juice like gamboge makes its appearance. The leaves are so heavy that the outstretched lateral branches are bowed under their burden, and sometimes even hang downwards. It is therefore unavoidable that many of these lateral branches should intersect and come into contact with each other, and that at the places of contact the epidermis should be wounded by the friction. But at such places an actual fusion of the branches occurs, and since this process is many times repeated, a lattice-work results, as shown in fig. 159. The individual portions of the latticed stem remain soft and pliant, and thus mutually supporting one another, the whole possesses a bearing capacity adequate to enable the erect shoots to rise higher and higher from this scaffolding. The lattice-work is additionally strengthened by the production of aërial roots from the older internodes. These, like the stems, fuse where they intersect. From their general external similarity it is often difficult to distinguish between the two sets of elements comprised in an old lattice-work. In cases where the inclosed stem increases in thickness, the latticed sheath becomes tightly stretched. Often, in *Clusia*, many of the branches die in consequence of this tension. Still, new shoots generally arise from the stumps, and repeating the already-described method of growth, become interlaced into a lattice-work. Sometimes the adherent stems become flattened and girdle-like, whilst aërial roots developing at many points become inextricably interwoven in the lattice-work till it is impossible to see the original palm stem. On the banks of the Rio Guama in Brazil, Martius saw whole groves of the Macaw tree (*Acrocomia sclerocarpa*) covered with *Clusia alba*. The *Clusia* formed an absolutely closed sheath bearing flowers and foliage, whilst 10 metres above the stately crown of the palm-tree projected.

The *twining* stem (*stirps volubilis*) is able to reach considerable heights by attaching itself to various objects and twisting spirally around them. In a state of nature, erect stems or even those of other climbing plants may serve as supports, whilst in gardens, sticks, strings and wires are utilized in this way when it is desired that twining plants shall cover walls, arbours, &c. We find by experience that even very fine threads form excellent supports, while thick posts and bulky tree-trunks are less adapted for this purpose. In the case of many annual twining stems, props of even 20–25 cm. diameter are too thick for the plants to twist around. Those perennial and lignifying stems called lianes are sometimes found round pillars of 30–40 cm. diameter, *e.g.* those of *Glycine Chinensis* in the avenues of the park at Miramare, near Trieste. In the tropics, twining plants are seen embracing the trunks of trees as much as 40–50 cm. thick, but in such instances it is probable that the trunk did not possess this thickness when it was first entwined, and only attained it later on. Of course this can only happen under particularly favourable circumstances, for most perennial, twining stems

cannot stand the severe strain involved — a strain which must occur whenever the tree, around whose trunk a perennial twiner has wound, increases much in thickness. The twining stems of the *Lonicera*, figured on p. 160, certainly do not increase in length after lignifying, and must, therefore, act as constricting coils on the young actively-thickening tree-stems, which they often strangle to

Fig. 159.—Palm-stem used as a support by the lattice-forming stems of one of the Clusiaceæ (*Fragræa obovata*).

death. Sometimes one finds the hard basal parts of a liane stem twisted and coiled apparently around nothing. This is due to the fact that the original support has been killed, and then slowly rotting into dust, has been denuded away by the wind and rain. Thus many a liane of the tropical forest seems to have made use, when young, of some living plant with a fairly thick erect stem as its first support, up which it has climbed into the crowns of higher trees.

Subsequently, the first, lower prop has perished, while the branches supporting the upper portion of the liane remain still vigorous and afford a good hold. An erect corkscrew-like liane stem is then seen hanging from the upper branches; it has a very odd appearance, and is only surpassed in the peculiarity of its form by the twined stems of bauhinias and monkey ladders, to be described presently.

But if the erect, young stem is stronger and more vigorous than the twiner which encircles it, which has been used as a prop, it does not allow itself to be strangled; the twiner is destroyed when they both increase in thickness. The coils of the climber are gradually stretched tighter and tighter, and many are the contrivances which exist for preventing the tension from immediately acting injuriously on the movement of the sap in the interior of the twining liane stem. As this thickening continues, the pull on the coils becomes so great that the death of the liane results. With its decay, the coils of the liane offer no further resistance to the enlargement of the stem within; but become ruptured and unravelled. It is clear from this that it is not always advantageous for perennial and lignifying twining stems to make use of active stems as supports, and it is also obvious why old and very thick tree-trunks are never seen—even in tropical forests—encircled by twining stems. But those growths whose twining stems persist only through a single summer, and either perish entirely after the ripening of seed, like those of the twining Polygonum (*Polygonum Convolvulus*), or else die down to the ground like those of the Hop (*Humulus Lupulus*), would suffer no injury even if they were to twine round thick tree trunks. Such plants which have to develop stems and leaves in the course of a short summer, and to manufacture by the help of their green foliage the materials necessary for the formation of flowers and fruit, must spring up from the soil to the sunny heights as quickly as possible and by the most direct path. This they can best do by using a thin thread as a support, certainly not by twining round a thick tree-trunk. The path round a thick trunk would be much too long; the material necessary for the building up of such lengthy coils would be needlessly expended, and such a waste would be entirely opposed to the economy of plant-life. Of course this does not imply that twining plants have the capacity of seeking out the most suitable supports, or of selecting the most desirable from amongst many. The capacity of selection is at all times only apparent, and if hop stems never twine round props of more than 10 cm. diameter, it is not because the hop shoots are able to recognize beforehand the unsuitability of large coils, but because with such extensive spirals they lose the power of firmly adhering to the stem. And with this we come to the description of the processes of adhesion and torsion of stems, so far as they are accessible to observation.

Like interweaving and lattice-forming stems, twining stems at first grow directly upwards. The lowest internodes still remain erect whatever may be the fate of those developing above them. After a sufficient number of successive

internodes have been formed, the number varying according to the species, those uppermost bend over laterally, and the whole shoot now consists of a lower erect portion fixed in the soil, and an upper overhanging portion which ends freely. The lower part forms a firm and reliable support, the upper bent portion, waving in the air, undergoes movements the aim of which is to revolve the free end round in a circle or an ellipse. This movement of the nutating portion of the shoot has been compared to that of the hand of a clock; still better, it may be likened to the movement of a pliant switch or whip which is held in the hand above the head and its end swung round in a circle. The nutation of the climber is not so quick as that of the revolving part of the switch, but is accomplished with a rapidity which astonishes the observer. In warm weather the waving, revolving end of the Hop (*Humulus Lupulus*) makes a complete revolution on an average in 2 hours and 8 minutes; the French Bean (*Phaseolus vulgaris*) in 1 hour and 57 minutes; the Bindweed (*Convolvulus*) in 1 hour and 42 minutes; the Japanese *Akebia quinata* in 1 hour 38 minutes; and the Chilian climber, *Grammatocarpus volubilis*, in 1 hour and 17 minutes. Since these revolutions are performed by fairly long portions of the shoot, they may, like those of the clock-hand, be seen with the naked eye, especially when a collar of white paper is placed on the shoot in the sunlight below the overarched portion. The shadow of the moving part, like the hand on the dial-plate, is then seen slowly but plainly advancing over the surface of the paper. In other twining plants the motion is of course much slower, and many of them occupy 24, or even 48 hours in a revolution.

Since in most twining stems a twisting of the extended fibrous bundles on the periphery of the stem occurs simultaneously with the circling of the free end, it was formerly supposed that this revolving movement was actually produced by this torsion of strands of fibres there situated. Very careful investigations in recent times have, however, demonstrated that this is not the case. The circling is produced independently of the torsion, and twining stems exist in which no torsion whatever of these fibrous bundles takes place.

We shall obtain the most accurate conception of the revolving movement of the tip of a shoot if we still retain our illustration of the movement of a switch swung round in a circle. When the switch, which may be best considered as a cylindrical body whose periphery is striped longitudinally with numerous straight lines running parallel to the axis of the cylinder, begins its motion, there is first of all an outward lateral bending. The side which becomes concave experiences a contraction, the convex side an elongation. Thus on the concave side a pressure, and on the convex a tension is set up. At any given moment these opposed strains are greatest along two opposite lines running along the periphery of the switch; in the next moment, however, the greatest strain passes over to the adjacent opposed lines, and since the greatest strain on the periphery of the switch moves in this way, and touches all the lines in succession, that remarkable circular movement of the free end of the switch results which

entirely resembles a torsion, but which, however, as a matter of fact, is connected only with a successive bending to all the points of the compass, and with no actual spiral twisting whatever. This movement may also be seen on a switch fixed in the ground, and, generally, in any pliant shoot, by bending down the top in all directions successively, so that the point describes a circle; thus it can be easily demonstrated that no spiral torsion in the tissue of the shoot is caused by the successive bending on all sides. This movement has received the name of *circumnutation*.

We may now proceed to inquire into the series of changes within the stem which cause it thus to bend in all directions, what must go on in the cells along one line in this stem to cause it elongate, along another to make it contract, and to bring about this successive elongation and contraction in all the peripheral longitudinal rows. Here unilateral pressure from outside, which so often causes curvature in other cases, is shown to be just as little the reason as unilateral illumination, which it is known also produces a curving of leafy stems towards the incident sunlight. When we see that the young branches of beeches are overhanging under their burden of leaves, we may think of explaining the matter by gravity; but how can we thus explain the enigmatical advance of the inclination towards all the points of the compass, which is the point at issue here, and which has to be accounted for? The phenomenon has also been referred to growth, and it has been said that it was caused by the various longitudinal lines on the circumference of the shoot successively growing more actively than the sides opposite to them. But even supposing that the whole matter was only a phenomenon of growth (which is certainly not the case, since many shoots make these revolutions without showing the slightest increase in length), the question why it happens that the stronger growth is transferred from one longitudinal row to another, would still remain to be answered.

The first step in an attempt at explanation is to consider similar phenomena where the conditions are much simpler and where the investigation is hindered neither by simultaneous growth nor by simultaneous torsion. As such phenomena we may regard the rotating movements of protoplasmic threads in swimming swarm-spores, the circular movements of the threads of Oscillatorieæ composed of disc-shaped cells like rolls of coins, and the similar movements of the whip-like filaments of numerous species of *Dasyactis* and *Euactis*. Here we may disregard the question of the end to be attained by these movements. This much is certain (1) that in the one case protoplasmic threads, and in the other simple rows of cells, exhibit in their revolving movements those advancing, opposed strains which we have just noted in the rotating switch; (2) that the elongation on the one side and the contraction on the other in all these filamentous structures are not produced by a direct external stimulus. This elongation and contraction, this enigmatical advance of inclination towards all the points of the compass can therefore be caused only by internal forces, and we must suppose that the living protoplasm of the whip-like thread spontaneously elongates and contracts, bends

and revolves in the manner described above. That which is performed by the naked protoplasm of a cilium may also be accomplished by the association of protoplasmic masses in the simple cell-filament of an oscillatoria-thread, and nothing contradicts the supposition that also in those extensive cell-aggregates which compose the shoot of a twining plant, the progressing, opposed strains, which appear as revolving movements in the shoot, occur in like manner. Why should not one portion of the masses of protoplasm, associated together and co-operating harmoniously for the welfare of the whole plant, perform that work which is accomplished in minute unicellular plant-organisms by an extended protoplasmic thread? Is it not simplest to suppose that the living protoplasm of certain rows of cells on the circumference of the shoot should effect the elongation and contraction, the advancing opposed strains above described, in a word, the twining movement of the whole shoot-apex? What it is that impels the protoplasm to this work is just as puzzling as the stimulus to the production of partition-walls in the interior of a cell, or the motive to those wonderful accumulative and divisional processes in the protoplasm of the Myxomycetes described on p. 572. We know, indeed, that these processes, which depend on the displacement of the ultimate particles of the protoplasm, are possible only under certain external conditions, but it cannot be asserted that external conditions definitely shape and direct the work done by the protoplasm.

In a number of twining plants, *e.g.* the Hop, Honeysuckle, and the twining Polygonum (*Humulus Lupulus, Lonicera caprifolium, Polygonum convolvulus*), the shoots turn round from the west through the south towards the east, which is termed turning to the right (dextrorse or counter-clockwise). Others, again, as, for example, the Scarlet-runner, the bindweeds, and various species of birthwort (*Phaseolus multiflorus, Convolvulus sepium, Aristolochia sipho*), turn round from the west through the north towards the east, and this is termed turning to the left (sinistrorse or clockwise). External conditions have no influence on the maintenance of these directions. It is a matter of indifference to the direction of these movements whether we allow light, warmth, and humidity to operate on this side or that; the particular species always twists in the same direction, the Hop towards the right, the Scarlet-runner towards the left. More than this, even if the twining portion is continuously bound in an opposite direction, the result is all the same; the plant cannot be coerced into any other path, and will not depart from the direction peculiar to it. It continues to twist and twine according to an innate tendency inherited from generation to generation, and we can only refer the different directions of twisting to internal causes, to the peculiar constitution of the living protoplasm in each particular plant.

However puzzling the ultimate causes of this torsion may be, the end to be attained by these revolutions of growing shoots is patent enough. That it may twine upwards a shoot requires an erect support, with which it must come into contact almost at a right angle. If such a support exists in the immediate neigh-

bourhood, this contact occurs at the very beginning of circumnutation, but when there are no erect stems close by, the shoot in its search bends its apex to all the points of the compass, and describes wider and wider circles with its increasing length. If in the space so traversed it finds no suitable support, the lower portion of the shoot falls on the ground and becomes a procumbent stem; but the middle portion again rises up, and the free end twists round in a circle afresh. The place where the nutation now occurs is removed some distance away from the spot where it first began, and perhaps the revolving shoot in its new position may strike against something which may serve it as a support. But if here also no suitable support is encountered, a further migration may occur; thus a comparatively extensive area is explored by the circling shoot in its quest for something to climb around. The phenomena just detailed gave rise to the view formerly held, that twining plants possessed the power of searching for a support, indeed, the idea was favoured that the twining stem was positively attracted by such support. But such a notion is disposed of by the actual facts. The meeting of the nutating shoot with an erect stem must be held to be quite accidental, still it is certain that this meeting is facilitated by the movements described above, and the probability of an erect stem being encountered is obviously greater the more extensive the space traversed by the shoot-apex.

As soon as the revolving end of the shoot comes into contact with an erect support of suitable thickness, it embraces the support, and adhering to it, twists round it spirally and assumes the form of an elongated spiral wound around it. This process may be illustrated by comparing it with the movement of a rope swung in a circle coming in contact with a post, that is to say, when one swings a long rope or a long whip horizontally with the hands raised above the head, and at the same time approaches so near to an erect post that the revolving rope must reach it, then that portion of the rope beyond the point of contact twines spirally round the post.

It has been shown by manifold observations and experiments that erect props are most easily embraced by twining stems. When the inclination of the prop amounts to not less than 45° with the horizon, the twining shoot still forms a spiral round it; but horizontal sticks are very seldom, though occasionally, entwined. It has also been ascertained that the revolutions made by the twining stem become both higher and steeper with increasing age. The coils formed by the youngest and uppermost portions of the shoot are often very close together and almost horizontal, but lower down the spiral appears more drawn out, and the newly-formed upper flat coils are gradually pushed passively upwards. Thus the advantage is obtained that the lower portion, as it assumes a steeper position, gets a better grip of the support. In most cases of twining the stem is to some extent twisted on itself, *i.e.* undergoes torsion. This torsion of the axis must not be confused with its twisting around the support. The two things are distinct. We can take two ropes, in one of which the strands are twisted, whilst in the other they are straight. Each of these may be wound round a support. The former (*i.e.* the twisted rope)

will have the best grip, as it is stiffer and its obliquely-running strands admit of a better hold. So it is with the climbing stem. By the torsion of its own axis it gets a better hold. The longitudinal ridges on its surface—due to its bundles—correspond to the strands of the rope. When these, by torsion, run obliquely, more purchase on the support is obtained.

Not infrequently the attachment of the twining stem is also strengthened by stiff, backwardly-directed bristles, and by barbs which are developed on the ridges, as is the case, for example, in the twining *Polygonum*, and in bean-plants. These reversed prickles are comparatively large in *Ipomœa muricata*, a species of bindweed. Hops also possess prickles of a remarkable form. In the Hop, as may be seen in fig. 160, they have the shape of an anvil; that is to say, a cell which is much extended in the longitudinal direction, and tapers to a point at either end, is developed on a peg-shaped or conical base. Its wall is silicified and very hard, and the points hook into softer tissue like claws. Such climbing hooks are found in regular rows on the six ridges of the twining hop stem, and are a great assistance in attaching it to the entwined support.

In *Hoya carnosa*, known for its waxen flowers, and often cultivated in greenhouses, the young twining stems are thickly beset with reversed hairs which under certain circumstances contribute materially to the adhesion to rugged substrata. Moreover, the stems of this plant, as soon as they have ceased to nutate, develop light-avoiding, climbing roots which nestle to the substratum and unite with it, thus adding to the security of the stem. The stems of *Hoya*, like those of *Cassytha* and *Cuscuta*, described on p. 171, are thus, in a way, intermediate between those of twining plants, in the strict sense, and climbing plants provided with clinging roots, which latter will be discussed presently.

When the nutating end of a twining stem has found no erect support in its neighbourhood, the older portions of its stem which no longer revolve take on, even without a support, a spiral twisting and a torsion of the axis. Just as a rope becomes more rigid when twisted, so the stiffness of these twisted stems, though they have no support, is increased in comparison with untwisted stems. Such a twisted stem may even rise a little above the ground, and in many instances the still nutating free end is enabled to reach some bough of a neighbouring tree or bush, and winding round it, to attain to the tree-crown. Many twining plants, as, for example, hops, frequently send up above the ground from their subterranean perennial portions several shoots. If these find no support in the ordinary way, they wind round one another, and a regular coil or cable is produced (*cf.* p. 364). These cables often rise without any foreign support to a considerable height above the ground, and thus single nutating apices are afforded the possibility of grasping a support which otherwise might have been denied them.

Should all these methods prove of no avail the twisted stem takes up its position on the ground; its growth is retarded, and it has the appearance of a stunted, sickly plant. This fact is in so far interesting because it seems to indicate that the pressure experienced by a twining stem adhering to a supporting prop has

a favourable influence on the growth of the shoot as a whole. This pressure must be regarded as a stimulus, just like the pressure which incites the tendrils, to be described below, to luxuriant growth. We may therefore conclude that twining

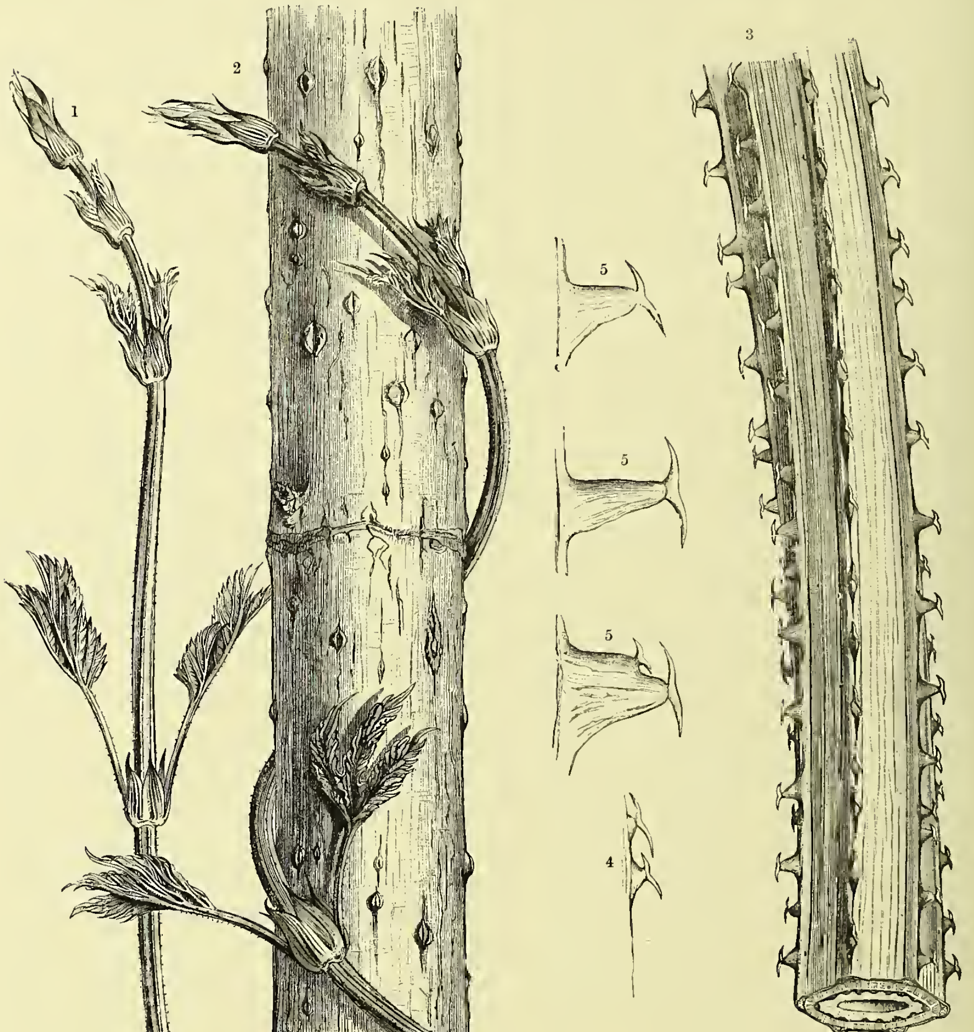

Fig. 160.—Twining Hop (*Humulus Lupulus*).

1 Free end of a shoot recently emerged above the ground. 2 Shoot of Hop twining round an elder-stem; natural size. 3 A portion of the Hop stem magnified. 4, 5 Single, anvil-shaped climbing-hooks detached from the stem; more highly magnified.

stems are irritable, although the irritability in this case is not so conspicuous as in tendril-forming structures.

In the temperate zones the majority of twining stems have only a short life. The twining *Polygonum* is an annual; hops and bindweeds are indeed perennial, but their stems sent up fresh each year from the underground stock always perish

in the following autumn. Only the Bitter-sweet (*Solanum dulcamara*) and several species of honeysuckle (*e.g. Lonicera caprifolium* and *Periclymenum*), which exist in comparatively inclement regions, possess twining stems which increase in thickness from year to year. But in many of these species the twining is not very conspicuous, and the Bitter-sweet forms, so to speak, a link between plants with twining and those with interweaving stems. In tropical regions, on the other hand, long-lived twining stems are by no means rare. Obviously the coils of a stem, firmly attached round a thin support and increasing in thickness, must approach one another very closely; thus arise those strange lianes which excite the astonishment of all visitors to tropical forests. Stems are quite common of a diameter of 4 cm.,

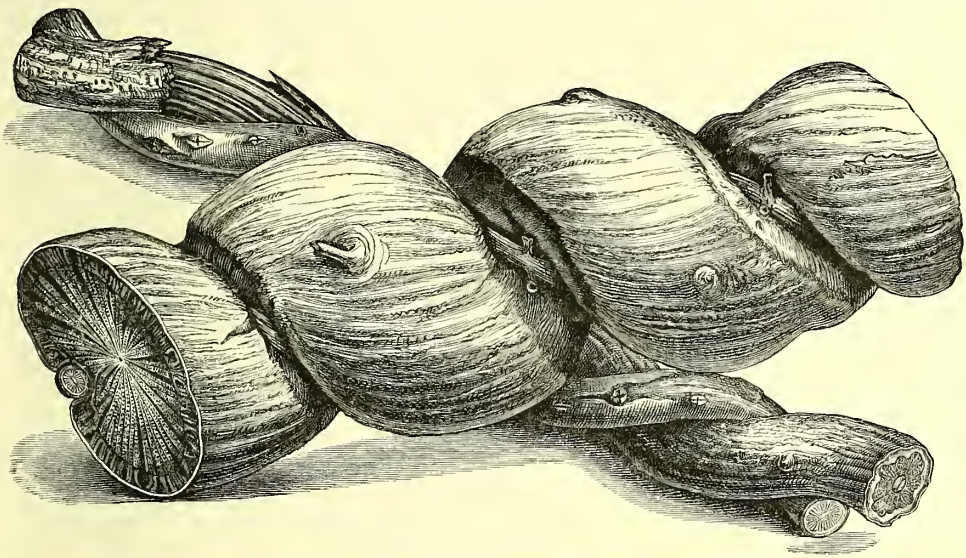

Fig. 161.—Portion of a Liane stem, twisted like a corkscrew, from a tropical forest; natural size.

wound like a corkscrew round the thin stems of other lianes, and sometimes such structures—of which a small portion is represented in natural size in fig. 161—are seen stretching right up to the summits of the trees in hundreds of uniform twists, like a thick ship's cable many metres long.

The *tendril-bearing stem* (*stirps cirrhosa*) climbs up into the sunlight by the help of special organs known as *tendrils*. The tendrils are filamentous structures when young; sometimes of exceeding delicacy, sometimes thick and stiff. In some cases they are simple, in others forked, but always sensitive, and so constructed that they can grasp any body with which they come in contact, hold it fast, and use it as a support. Before the tendril adheres to a support it is straight, and extends in the direction in which there is the greatest probability of reaching a support. It also performs movements the aim of which is to strike against some firm object. If this end is attained, the support which it has encountered is firmly gripped by the tip of the tendril, whilst the part lying immediately behind the point of attachment contracts together spirally. By this spiral contraction the

stem from which the tendril arose is drawn towards the support, and is, as it were, attached to it by a spiral spring.

Tendrils are always produced in numbers from the stem. Usually one, sometimes two tendrils arise from each of the upper nodes, and with the exception of the lowest portion, which is usually quite without them, the stem is very regularly

Fig. 162.—Stipular tendrils of the common Smilax (*Smilax aspera*).

beset with tendrils along its whole length. The advantage of this is that in case one tendril should fail or find no support, a neighbouring one can always take its place. Generally plants with tendril-bearing stems are at a decided advantage in comparison with all other forms of climbing growths, which explains the fact that their number is in considerable excess of the others. In climbing over a shattered rock-face or thick tree-trunk they have a great advantage over plants with twining stems. In some cases the tips of the tendrils fasten on even to the smoothest rocks by peculiar discs, or they grip and hold fast to small projecting portions

of bark and the stumps of broken twigs, things which are impossible to twining stems. Tendrils preferably twine round horizontal twigs and leaf-stalks, and frequently round old tendril-bearing stems which have previously climbed up to the crown of a tree. When they have reached up to the branches, they can pass over from one bough to another, fasten themselves firmly above and below, and so gradually invest the whole of the crown. From the summit fresh shoots arise

Fig. 163.—Leaf-stalk tendrils of *Atragene alpina*.

which curve downwards and are swayed by the lightest breath of wind; from them new tendrils project, like the tentacles of some sea-monster, and if one of them but touches a leaf-stalk or twig of a neighbouring tree, it curves round it and grasps it firmly. Very soon a second, third, and fourth tendril will similarly become attached, and, contracting spirally, will pull the pendent shoot up to the neighbouring tree-crown. The bridge so formed is again used as a means of transit by other climbing stems, and thus arise garlands and festoons, which hang from tree to tree; whilst not infrequently an actual arcade is formed whose roof,

formed of tendril-bearing stems, is borne by two adjacent trees or thickets as though by two gigantic piers. Another advantage which tendril-bearing stems have over twiners consists in the fact that they can reach the same height above the ground with less expenditure of material. The twining stem of the Scarlet-runner, which has climbed a metre above the ground, shows, when unrolled, a length of $1\frac{1}{2}$ metres. The pea, which climbs with tendrils to the same height, is little more than a metre long. Of course in the production of tendrils building material is expended, but this bears but a small proportion to that which is required for the extra half-metre of stem.

Now as to the nature of tendrils, are they leaf, stem, or root? They may be each of these according to the species in question. A tendril may even be formed by metamorphosis from each of the different sections of a leaf independently, and the leaf-blade, the mid-rib, the leaf-stalk, even the stipules themselves may become tendrils. From the standpoint of development and with regard to the origin and mutual relation of individual plant-members, the exceedingly manifold tendril-structures have been classed generally in the following groups. First of all the *stipule-tendrils* (*cirrhus stipularis*), of which species of smilax (*Smilax*) afford an excellent example. As may be seen in *Smilax aspera* (see fig. 162), so common in the region of the Mediterranean flora, the leaves are divided into lamina, leaf-stalk, sheath, and stipules, and the two stipules arising from the sheath are transformed into rather long tendrils which surround the branches of other plants, and even their own branches.

More common than this rather rare form is the *leaf-stalk tendril* (*cirrhus petiolaris*), which itself again shows numerous modifications according as to whether the whole leaf-stalk of an undivided leaf, or the stalks of single leaf-segments play the part of tendrils. The former is seen very beautifully in the numerous species of Nasturtium (*Tropæolum*) and in the tendril-bearing snap-dragon (*Antirrhinum cirrhosum*); the latter in many species of fumitory (*Fumaria*), in the Traveller's Joy (*Clematis*), and in the only liane of the European Alps, the *Atragene alpina*, illustrated on the last page (fig. 163). In pitcher-plants (*Nepenthes*) a portion of the leaf-rachis is transformed into a tendril, and by it the pitchers are suspended on the branches of supporting plants (*cf.* fig. 24, p. 133). When the midrib of a foliage-leaf projects far beyond the green tissue of the blade, as a filament which grasps and surrounds firm supports and attaches the whole plant to them, this structure is known as a midrib-tendril (*cirrhus costalis*). To this class belong the strange South American mutisias (*e.g. Mutisia ilicifolia, hastata, subspinosa, decurrens*), the Indian *Flagellaria Indica* and *Gloriosa superba*, and several fritillaries (*Fritillaria cirrhosa, verticillata,* and *Ruthenica*), attaching themselves to stiff culms and leaves of neighbouring grasses. The *leaf-tendril* (*cirrhus foliaris*) is also interpreted as the midrib of a leaf-blade or of a leaf-segment, but here none of the green tissue of the blade is developed, and only the midribs are seen to form filaments which curve and fasten as soon as they come into contact with a prop. This form of tendril is the commonest of all, and is found particularly in Papilion-

aceæ in great variety. Sometimes the whole leaf-blade is metamorphosed into a single tendril, as in the Yellow Vetchling (*Lathyrus Aphaca*); but usually tendrils are formed only in the place of the terminal leaflet and of the upper leaflets of the pinnate leaves, as may be seen especially in vetches, peas, and lentils (*Vicia, Pisum, Ervum*). It should be mentioned here that in proportion as the green tissue of the leaf-blade is reduced in consequence of the formation of tendrils, the amount of

Fig. 164.—Branch-tendrils of *Serjania gramatophora.*

green tissue of the lowest leaflets, leaf-stalks, and stipules increases; in other words, that when tendrils appear in place of the upper leaflets, the lowest pair of leaflets and the stipules form large green laminæ. In many vetches even the stem and leaf-stalks are beset with green leaf-like bands and wings.

By a *stem-tendril* (*cirrhus capreolus*) is meant one which can be interpreted as a stem-structure, and a distinction is drawn particularly between *branch-tendrils* (*cirrhus rameaneus*) and *flower-stalk tendrils* (*cirrhus peduncularis*) according as to whether the tendril is to be regarded as a metamorphosed flower-bearing or

foliage-shoot. Flower-stalk tendrils are found in particular in grape-vines and in species of *Cissus*, in *Passiflora cirrhiflora*, in several species of the genera *Paullinia* and *Cardiospermum*; branch-tendrils in *Fumaria claviculata*, and in numerous gourd-like plants. These tendrils, of which the *Serjania gramatophora* (*cf.* fig. 164) may be taken as an example, arise usually not from the true axil of a foliage-leaf, but are displaced, pushed to the side of or below the subtending leaf; frequently even opposed to leaves which one might think really subtended them. This displacement is particularly striking in vines and gourd-like plants, for which reason these tendrils were formerly explained not as stems but as leaf-tendrils. Finally we must consider here the *root-tendrils* (*cirrhus radicalis*), which really are roots arising from the foliage-stem, but in regard to their activity behave exactly like tendrils, and are chiefly observed in climbing, delicate-stemmed lycopodiums.

This classification of the manifold tendril-developments, useful for the speculative doctrine of form, and also to the descriptive botanist, has only a secondary value for the questions which are discussed in this book. It gives no conclusion concerning the significance which the different forms have with regard to the habitats of climbing plants, and it offers not the slightest assistance to our understanding how the stem is fastened to the support by the tendril arising from it. Tendril-bearing stems are extremely wonderful in this respect, and the different methods require a detailed description. For the purpose of this description we classify tendril-bearing stems into three groups, viz. into those with ringed tendrils, with nutating tendrils, and with light-avoiding tendrils.

Stems with *ringed tendrils* are especially adapted for climbing up between the erect and much-branched growth of dense hedges, copses, and low woods. Some of them are annual and do not rise far above the low underwood and shrubs, *e.g.* various species of fumitory and nasturtium (*Fumaria* and *Tropæolum*). Others, *e.g.* the Traveller's Joy and Atragene (*Clematis* and *Atragene*) are perennial; their stems become woody, often attaining to a considerable age, and the youngest branches of the old stems may climb up to the tops of trees. When one sees these plants hanging rope-like from the summits of tall, unbranched forest-trees, one may conclude that they first became fastened to them at a remote period, when the trees were still quite small, and that they have ever since kept pace with them in their growth. The young shoots of such climbers with their leaves still small, erect, and folded to the stem, appear capable of pushing through even very small gaps in the thickest undergrowth, thus reminding us strongly of the manner of growth of interweaving stems. They also agree with interweaving stems inasmuch as they form actual anchor-arms by extending and reflecting their leaves and leaf-stalks by whose help they suspend themselves on the horizontal branches of the supporting undergrowth. This is the case in *Clematis* and in the Atragene illustrated in fig. 163,—these plants having opposite leaves whose stalks project from the stem almost at a right angle. The stalks and blades of the leaflets, also, complete the semblance to the arms of an anchor, since the former sink down at an obtuse angle with the main

stalk, whilst the latter, after the laminæ are unfolded, curve like an arch, forming an actual loop.

As already stated, no distinction can be recognized in the earlier stages between interweaving stems and those with ringed tendrils. The difference first appears as soon as the lower side of the leaf-stalks comes in contact with a branch of the undergrowth. This contact, if it is not of too transient duration, acts as a stimulus on the leaf-stalk, and the result is that it curves round the branch and grips it like a ring. The stalks always curve towards the side which has been touched, or pressed. Since the leaf-stalks are equally sensitive on all sides, the curvature may take place above or below, or laterally, according to whichever part has been stimulated. Even continuous contact with flower-stalks of hair-like delicacy is sufficient to produce the ring-formation, and it has been shown by experiment that the continued pressure of a thread weighted up to four milligrams is followed by a curvature. The stimulated leaf-stalk usually forms one or two, less often several annular coils on the branch embraced, as shown in fig. 163. It also frequently happens that neighbouring stems of the same plant are connected together by their tendrils and twined into inextricable knots. The conversion of the irritable leaf-stalk into an effective, gripping tendril in many of the plants in this group is materially assisted by the fact that the younger portions of the shoot revolve in circles like those of twining stems, though less regularly. Thus a much-increased number of suitable objects in the environment become possible as supports. These leaf-stalks, which become tendrils, do not, however, themselves nutate, consequently they are clearly distinguished from those of the following group, which are called nutating tendrils.

Stems with *nutating tendrils* have not the power of climbing up rocky walls or the bark of thick tree-trunks, and, like the foregoing, are only able to use as supports culms, leaves, and thin branches of other erect plants, to which they adhere and up which they are drawn by means of the spiral curvature of the attached tendrils. Plants equipped with this class of tendril require far more light than those with ringed tendrils, and they find their best and most favourable habitat in the open country dotted with isolated groups of trees, or on the edges of a forest bordered with bushes, and in sunny meadows studded with shrubs. They have not to interweave through the interlacing branches of an underwood; ringed tendrils are suitable there, but not tendrils with long nutating filaments which could either not accomplish their movements in the midst of the thick brushwood, or if they did, would not attain the desired end, viz. the subsequent elevation of the stem.

The lowest portions of the young shoot possess no tendrils, and they are kept erect solely by the turgescence of their tissues. In many species the stiff, spreading leaf-stalks, or the peculiar barbed leaf-blades help to support the young shoots on the neighbouring plants and to keep them erect. But these supports are but temporary measures, and the upper portion of the shoot soon develops tendrils. These elongate quickly and get to work. The filaments of these tendrils elongate with extraordinary rapidity, straighten out, and then project like tentacles far beyond the foliage-leaves. At their tips only do they exhibit a more or less hook-like

curvature (*cf.* fig. 165). When they have reached their full length they begin to move round in a circle just like the apices of twining stems. If by this movement they meet with an object suitable for a support, they grasp and embrace it by their hooked ends. That is to say, contact with a foreign body acts like a stimulus on the tendril; it loops itself over the object with which it is in contact, and then rolls up in a spiral, thus drawing the stem, which bears it, obliquely upwards. Now

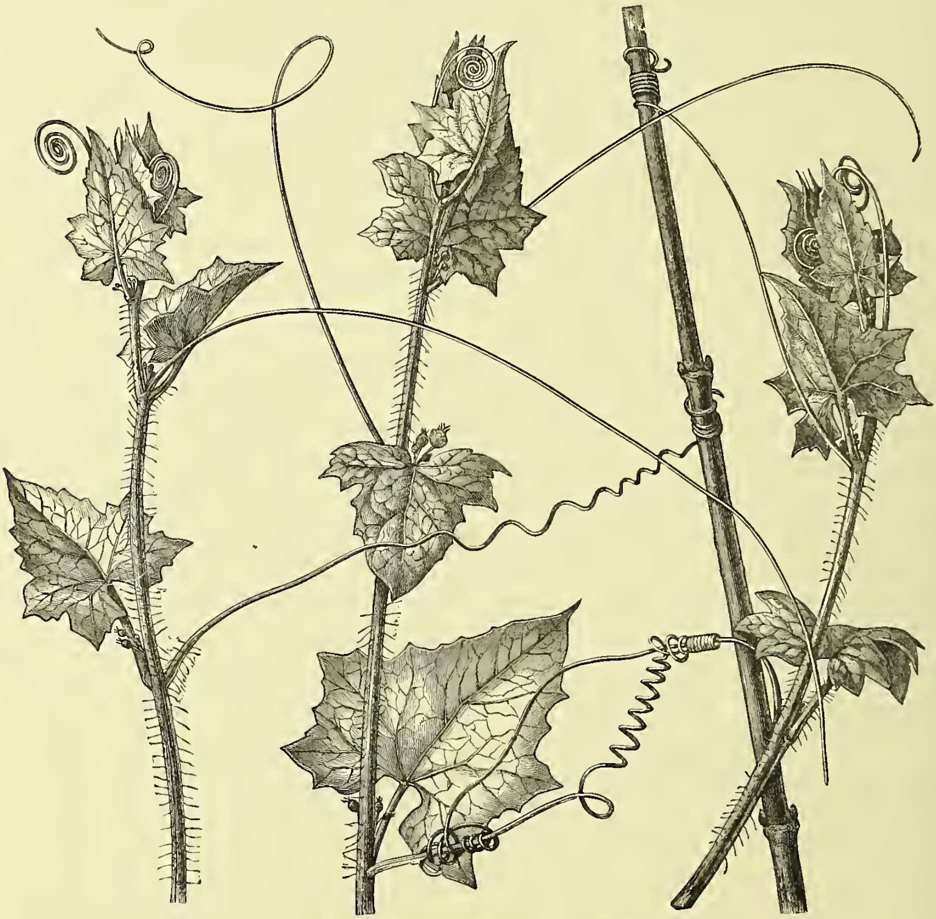

Fig. 165.—Tendrils of the Bryony (*Bryonia*).

comes the turn of the tendril inserted next above. This behaves exactly in the same way as the first, and in a very short time is succeeded by a third, fourth, &c. It does not much matter if in its nutation one of these tendrils should have found no support, since the successive tendrils are placed so close to one another, and replace each other so quickly, that the shoot is still drawn up uniformly, and is prevented from falling. When whole series of tendrils find no places of attachment, the shoot of course falls down, under which circumstances possibly one of its tendrils may encounter a distant branch to which it can fasten, and which it can use as a support. If this should fail, the tip of the pendent shoot again rises up, sends out

fresh, nutating tendrils, and so may still succeed in grasping some projecting twig in the neighbourhood upon which it can climb. The paths traversed by such tendril-bearing stems are therefore often wound oddly hither and thither, but the stem always follows the periphery of the bush or tree-crown which it has selected, and the inner branches of these supports are never interwoven by it. Plants whose tendril-bearing stems ramify strongly may invest the whole tree over which they grow with an actual mantle, and if the climber in question has large leaves, it may be quite impossible to determine from outside what species of plant has become thus enveloped.

The account given above deals only with such phenomena as are displayed by all tendril-climbers in common; but in individual cases there are innumerable special contrivances, which it would be impossible to describe in detail in the limits of this book, and I must therefore be content with enumerating some of the most striking that have been observed.

First, it has been pointed out that in many cases, for example, in the tropical passion-flowers, not only the young, extended tendrils, but also the whole shoot-apex revolve in circles thus widening the space traversed by the tendrils, and increasing the probability of meeting with a support. If the tendrils are forked, each of the two branches performs its particular oscillations, as can be seen, for instance, in the tendrils of the grape-vine. The period of revolution, taken by a nutating tendril, varies very much according to the species. *Cobœa scandens* takes only 25 minutes, *Passiflora sicyoides* 30–46 minutes, and *Vitis vinifera* 67 minutes for a revolution. The rapidity with which the tendrils curve in consequence of the pressure exercised on them by a foreign body which acts as a stimulus also varies very much with the species. In *Cyclanthera pedata* the curvature commences 20 seconds after contact with a hard stick; in passion-flowers (*e.g. Passiflora gracilis* and *P. sicyoides*) after the lapse of about half a minute, in *Cissus discolor* after 4–5 minutes. If the stick with which the tendril is in contact is removed, the curved portion straightens out again. If it is left in contact, the curvature proceeds uniformly. In *Cyclanthera pedata* the first complete coil around the support is accomplished in 4 minutes, in others, on the other hand, it may take several hours, or even 1–2 days. Usually the tendril is not content with a single coil, but forms several of them. The coils are closely pressed to the prop, and in their growth adapt themselves like a plastic mass to all its projections and depressions; the substance of the tendril even penetrates into the small clefts and crevices, and when the tendril is detached from its substratum, an actual cast of all the inequalities of the support can be seen on its contact-surface. In many species, *e.g.* in *Hanburya mexicana*, peculiar callus-like growths arise here. The ends of the tendrils, as already stated, are curved like a hook so as to more easily grasp the object to which their circling movement brings them. In many species the tendrils terminate in actual claws. The tendrils of *Cobœa scandens*, a native of Mexico, but frequently grown as a decorative plant in our conservatories, are specially elegant. They are leaf- or midrib-tendrils, and divide repeatedly in the most beautiful manner. Each of the ultimate branches

bears a double claw whose points immediately fasten into any object at the slightest touch, and will even remain suspended in the skin of the hand. The three delicate branches of the tendril of *Bignonia venusta* also end in pointed claws which resemble those of insects' feet. The majority of tendrils are branched, whilst simple undivided filaments, as shown in the *Bryonia* (fig. 165), are comparatively rare. Passion-flowers and gourd-plants have the longest tendrils, those of the common gourd (*Cucurbita pepo*) often measuring more than 30 cm. in length. The spiral contraction of the part of the tendril not wound round the support begins, according to the species, half a day, or one or two days after the apex has formed the first coil round the support, but it is very quickly accomplished when it has once begun. This torsion is sometimes towards the right, sometimes towards the left, and frequently it is accomplished partly in one direction and partly in the other, by the same tendril. The number of twists formed in this spiral contraction is very variable. In the long tendrils of some gourds as many as 30 or 40 are produced. By these spiral springs the fastening of the stem to the support is excellently accomplished; it is at once adequately attached to the support, but not pressed to it, consequently unnecessary friction is avoided. During a blast of wind there is a certain amount of "give", but directly the gust subsides, the climber—thanks to its elastic tendrils—resumes its former position. This spiral twisting occurs also in tendrils which have not succeeded in grasping a support, but strangely enough, they become stunted, shrivel, and wither, sometimes becoming detached from the stem like autumn leaves. Those tendrils, on the other hand, which have embraced a support become much stronger and thicker, and also undergo a series of changes in their inner structure which adapt them excellently to the part they have to perform.

Stems with *light-avoiding tendrils* remind us of the light-avoiding interweaving and lattice-forming stems, and, like these, are found in plants which have to climb up steep rock faces and over the bark of large trees. In these cases the more or less plane surface of the rock or tree-trunk is the only support afforded for climbing. The stem on such a substratum would extend its tendrils in vain on the side where there is only the air to be met with; here there is no resting-place or support which can be reached by circling movements. The best the tendril can do under the circumstances is to seek out the solid wall along which the stem has to climb as quickly as possible. In such cases the desired support is on the side turned away from the light, and as a matter of fact, the tendrils of these plants turn towards this side with great persistence. According to the position of the point at which the tendril springs from the stem, it curves at an angle of 90–180° in less than 24 hours, and grows towards the background without digression and without wasting its energy in revolving movements. The leaves of the same plant, for exposure to light and air, are extended in a direction away from the wall, and try to assume the position most favourable for this purpose. The path it has taken soon brings the tendril in direct contact with the wall, with which it now has to obtain a firm hold. This it does either by peculiar adhesive discs, or by wedging itself

into the dark clefts and crevices existing in the supporting wall. Several species of the genera *Cissus, Vitis,* and *Ampelopsis* develop adhesive discs. In the *Vitis inconstans,* a native of Japan and China, and known among gardeners by the name of *Cissus Veitchii* (figured on the right-hand side of fig. 166), as soon as the tips of the tendrils, which are provided with tiny knobs, come in contact with a hard wall, they spread out, just like the toes of a tree-frog. In a very short time disc-like pads are formed from the knobs, and these become cemented to the substratum by means of a sticky fluid mass secreted from the cells of the disc. This cement now holds so fast that on trying to separate the tendril from the substratum it is much

Fig. 166.—Light-avoiding Tendrils

1 *Vitis (Ampelopsis) inserta.* 2 *Vitis inconstans.*

more likely that the tendril-filament will be torn than that the disc will be detached. *Vitis Royleana* and *Ampelopsis hederacea* (the Virginian Creeper) also develop these adhesive discs, but here they are not prefigured by knobs on the branches of the tendrils as in *Cissus Veitchii*; the ends are curved like hooks, and are barely thickened. As soon as they reach the hard wall the tendril-branches diverge, spread out on it laterally, and arrange themselves at definite intervals in the most advantageous manner. Within two days the curved apices thicken and turn crimson, and in another two days the discs are complete, and the tendrils are cemented by them to the wall. These plants can climb up smooth walls, and even planed wood, glass, and smooth, polished iron are not rejected as substrata.

Bignonia capreolata, and *Vitis* (*Ampelopsis*) *inserta* (whose tendrils are represented in fig. 166[1]) behave differently from the three tendril-plants just mentioned. Here the curved tips of the tendrils, growing towards the wall, seek the crevices

and crannies of stone or bark and actually creep into them, or when only shallow grooves are to be found in the substratum, bury themselves in them. Smooth surfaces are avoided as far as possible since they afford no suitable hold to this class of tendril. When established in the chinks and crevices, the ends, which until now have been hooked, swell out like a club or ball, and in a short time thicken so much that they occupy the entire crack. It looks as if melted wax had been poured into the crevice and had then solidified and fitted itself to all its inequalities. The growth of the tissue extends, according to the depth of the crack and the nature of the contact-surface, over a sometimes larger, sometimes smaller portion of the embedded part of the tendril, and sometimes a callus-thickening is seen to arise even behind the apex, at places where the tendril has adhered closely to a small projection of stone. The thickened end of the tendril clings so firmly to the depression into which it has wedged itself, that it is very difficult to remove it; and here also the attachment seems to be completed by means of a secreted cement. It is seen on examining the parts of the adhesive disc or of the wedged callus-thickening which adhere firmly to the substratum, that the epidermis in particular has undergone a remarkable change. The epidermal cells are enlarged, drawn out as wart-like protuberances or conical projections, and adapt themselves to all the elevations and depressions of the substratum, grasping even microscopic projections, so that the contact-surface, after being detached by chemical agents, resembles sealing-wax against which a seal has been pressed while it was in a plastic condition.

It is remarkable that these adhesive discs and growths of callus are only developed after contact with a solid body. If from any cause the tendril is prevented from coming in contact with a solid substratum, the growth of tissue, the development of papillæ on the epidermis and the secretion of a cement-substance do not occur, and the end of the tendril dries up and dies. This process reminds us strongly of the formation of weals on human skin, and, like this, is dependent upon stimulus, friction, and pressure.

A spiral torsion occurs in the light-shunning tendril as soon as it has become attached in one way or the other to the substratum. The attached tendrils now become much stronger, and always much more vigorous than those whose apices have not found a resting-place. The stem is now fastened by the elastic tendril to the steep rock face or fissured back of an old tree-trunk. Strong winds may drag the stem somewhat away from the wall, but when they subside it again resumes its normal position, as in the cases previously described, by means of the elastic tendrils. If the stem subsequently grows in thickness the spiral springs holding it are drawn out just as far as is required. Very old stems no longer need their clinging organs; they stand, as strong erect stems, in front of the wall up which they had years ago clambered as young shoots, although their tendrils have now been long dried up; the young shoots alone, always striving higher and higher, still continue to climb up the substratum in the manner described.

The *climbing stem* in the restricted sense (*stirps radicans*) holds itself in the normal position attained by growth by means of climbing roots, and uses as supports

the trunks of old trees, steep walls of rock, and under cultivation often wooden planks and palings. All these climbing stems have two kinds of roots—absorbent roots, by means of which they suck up fluid food, and climbing roots, which serve to maintain them on their supports. In most instances the functions of these two kinds of roots are kept distinct, so that a climbing stem soon withers and dies when it is cut across above the absorbent roots, although affixed to a rock or to the bark of a tree by a thousand climbing roots. But in a few cases the climbing roots will under these circumstances begin to absorb, provided, of course, that the substratum to which they adhere is able to afford them the necessary food.

In many respects climbing stems agree with the group of tendril-bearing stems just described, especially in the fact that the organs which furnish the adhesion to the support turn from the light, and also inasmuch as the adhesion to the support is brought about by a viscous substance either secreted by the cells in contact or produced by the breaking down into mucilage of the outer layers of the walls of these cells. The avoidance of light by all climbing roots is an extremely interesting fact. Whether the stem which forms climbing roots nestles close to its substratum, or some spans distant from it, whether it grows upwards along a stone wall or is deflected to one side by some obstacle—in all cases the first rudiments of the climbing roots make their appearance on the side of the stem turned away from the light. And when these small cushions develop into root-fibres, the direction assumed by their growth is always away from the light and towards the dark background. The darker the place, the more vigorous do the root-fibres become. When the climbing roots developed by *Tecoma radicans* (figured on p. 479) in the darkest places under a projecting ridge are compared with those which have been formed in less shaded places below, it is seen that the former are always much more luxuriant and longer than the latter. If by chance a shoot which has already begun to develop climbing roots is moved from its position so that the hitherto shaded side is exposed to the light, it twists round until the side with the rudiments of aërial roots is again turned from the light. If obstacles lie in the way of this torsion, the young climbing roots thus exposed remain undeveloped and grow no further; ultimately they wither and dry up.

As soon as the climbing roots originating from the shady side of the stem come into contact with the substratum below them their growth is noticeably increased, and in a very short time they become firmly united to it. Not only do the rootlets grow into all the crevices of the substratum and adapt themselves most accurately to its larger inequalities, but each single epidermal cell of the growing rootlet exhibits a like behaviour, fits itself to the smallest projections and depressions, and spreads out on entirely smooth surfaces like a plastic mass. Sometimes the epidermal cells are drawn out like tubes and form so-called root-hairs, these penetrate into the smallest clefts of the substratum and spread out like a hand whose palm and outspread fingers press against the soil. These epidermal cells of climbing roots also unite with the supports against which they have placed themselves like the absorbent cells described on p. 87, and the union is so firm that the roots are

much more likely to break off at the base than the united surfaces to separate when the roots are forcibly displaced.

The following types of climbing roots may be distinguished according to their shapes. First densely crowded, simply or only shortly branched, filamentous roots, arising in groups, but each separately from the stem; these are increased in number by the production of new batches as the lignifying stem becomes older and thicker, and they sometimes grow together and border the stem, adhering to the substratum in irregular, membrane-like rows. On older stems the climbing roots are usually for the most part dried up, and those which have not united with the support then project from the sides, often forming shaggy beards, and giving a very odd appearance to the stem. The Ivy (*Hedera Helix*, of which old stems are shown growing up on an oak in fig. 167) may be taken as an example of this type.

The second form presents a wholly different aspect; as the type we may select the *Tecoma radicans*, a native of the southern United States, often used for covering garden-walls. The climbing roots here are strictly localized. At each node of the shoot below the point of insertion of the leaves a paired cushion-like structure arises, and from each of these cushions several rows of protuberances, which grow out into as many rows of unbranched or shortly-branched, fringing fibres, 1–5 cm. long (see fig. on p. 479). The epidermal cells of this fringe, which come into contact with a firm substratum, elongate and form root-hairs, that is, papillæ and tubes, which in a very short time fasten to the support; after this they turn brown and die, thus never functioning as absorbent organs.

A form materially differing from these is shown by the climbing roots of the cactus *Cereus nycticalus*, known as the "Queen of the Night", which is represented in Plate VII. (facing p. 641), and also of several tropical Bignoniaceæ, and especially in *Ficus stipulata*, so often used in greenhouses for covering the walls. In the last-named plant the climbing roots arise in fascicles in the shade of the green leaves; they are filamentous and terminate in many hair-like, spreading rootlets. They adhere by root-hairs to the substratum, and thus fasten to it the tender, pliant stems. These roots are not very long and soon dry up, but close behind them much stronger roots arise from the stem, which has meanwhile become thicker, and these traverse the walls like cords, repeatedly branching and intersecting, and form actual net-works, often becoming several metres long. These latter roots do not help much in fastening the stem to the supporting wall; they are absorbent roots, and take up the atmospheric water, with its abundance of food materials, which has condensed or trickled down the bark of trees and rock walls.

The clasping roots borne by the stems of *Wightia*, a genus of Scrophulariaceæ growing in the mountainous regions of the Himalayas, and of several species of fig in the same district, may be regarded as a fourth type. The attachment of the young shoots is brought about here as in the form just described by the finely-branched but not much elongated roots, which soon dry up. But when the climbing stem begins to thicken much stronger roots arise which surround the supporting tree-trunk like clamps and actually engirdle it. These girdle-like clasping roots

Fig. 167.—Ivy (*Hedera Helix*) fastened by climbing roots to the trunk of an Oak growing in the woods near Heidelberg.

often fuse at the places where they adjoin one another and increase in circumference, frequently becoming as thick as a man's arm. The illustration on the next page (fig. 168), taken from a photograph at Darjeeling in the Himalayas, shows these stems, which look as if they had been actually tied on to the smooth trunks of tall trees, and which bend away somewhat from the support, and then ramify and develop abundant leafy branches.

Many tropical species of fig, which may serve as representatives of a fifth type, exhibit the following peculiarities:—their climbing roots, nestling to the substratum, flatten and spread out like a doughy plastic mass; the adjacent roots fuse together, and in this way irregular lattice-works, or incrusting mantles, only interrupted here and there by gaps, are formed, which lie on the supporting trunks and are firmly fastened and cemented to them without fusing with it or deriving nourishment from it. Frequently not the trunk only but the branches of a tree serving as support are incrusted with the flattened clamping roots of the climber. Sometimes the climbing *Ficus* sends columnar aërial roots down to the ground, whilst its leafy branches intersect those of the supporting tree; so complete is the entanglement that at first sight it is hardly possible to distinguish what belongs to the support and what to the climbing plant. Fig. 169 is a faithful reproduction of a sketch by Selleny drawn at Kondul, one of the small Nicobar Islands, showing one of these remarkable climbers with flattened roots incrusting the support, *i.e. Ficus Benjamina* on a supporting myrtaceous tree, the latter obviously suffering under the burden of its oppressor, and already in a dying condition.

These "tree constrictors", as one might call them, although they do not absorb materials from their supports, as was formerly supposed, are certainly not indifferent to them, and may injure and even kill them like the constricting, twining stems described and figured on pp. 159 and 160. The entwined tree decays and its wood disintegrates, perhaps termites assist in carrying away the remains of the dead trunk, but the climbing stem with the flattened, climbing roots remains still vigorous. It has meanwhile created a sufficient support for itself by its prop-like aërial roots, and these prevent it from falling. As Hooker says in his *Himalayan Journals*:—"We found great scandent trees twisting around the trunks of others and strangling them: the latter gradually decay, leaving the sheath of climbers as one of the most remarkable vegetable phenomena of these mountains". When at length the climber, deprived of its original support, also dies, its roots and stem-structures become bleached, and its curious forms, in which to speak with Martius, "the excited imagination fancies it recognizes fantastic spectres and gigantic voracious monsters", rise up weirdly against the dusky background of the primeval tropical forest.

The manner in which climbing roots become fixed upon their supports is not less varied than their manifold structural modifications. It has already been stated that the climbing roots are light-avoiding, and that their growing points are directed towards the rocky faces and boughless tree-trunks upon which they climb. Should the distance between the stem and the wall be not great, the

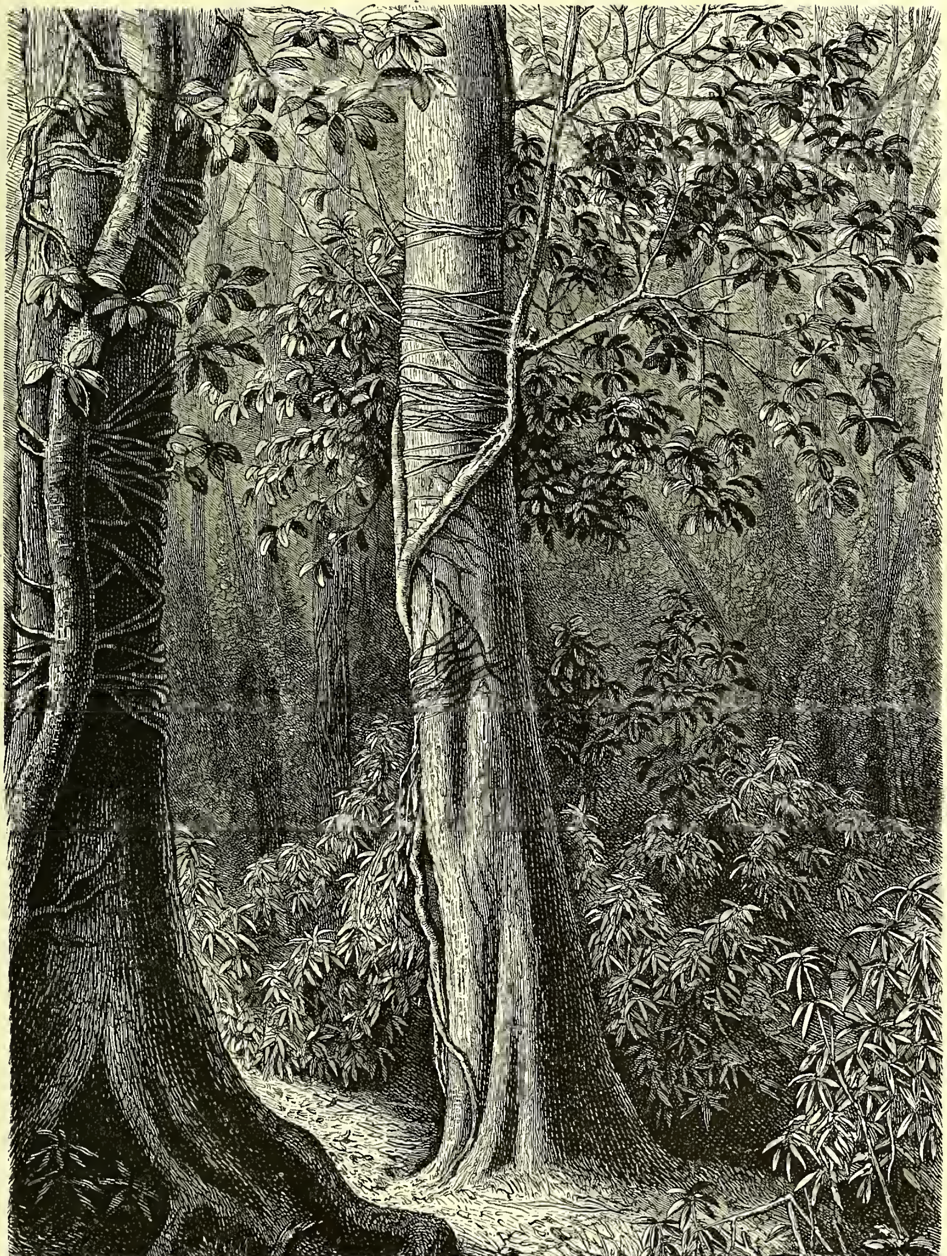

Fig. 168.—*Ficus* with girdle-like clasping roots, at Darjeeling in the Sikkim Himalayas. (From a photograph.)

climbing roots grow out directly to the wall. This is usually the case with climbing plants. Several Aroideæ and species of *Ficus*, and especially our ivy (*Hedera Helix*), the shoots of which occur anywhere at the foot of a tree-trunk or

of a rocky wall, develop climbing roots close below the growing shoot-apex. These roots speedily reach the wall and fasten the portion of the stem from which they arise to it. This continues slowly, the shoot-apex continually creeping higher up over the substratum. This is the simplest way in which climbing stems become attached. The process by which those of the often-cited *Tecoma radicans* are affixed is much more complex. These stems shun the light in a marked degree. If *Tecoma radicans* is planted in front of a wall covered with trellis-work, the actively growing shoots turn away from the light, slip behind the trellis-work, and adhere closely to the wall by those portions of the stem at which climbing roots appear. So soon as they come in contact with the hard substratum the small pale rootlets grow out from the cushions as a fringe of threads which cling very firmly to the wall. The growing shoot never leaves the wall, but keeps close to it, always seeking the darkest places under projecting tiles, ledges, and cornices, attaching itself at intervals by fresh clamp-roots.

The most remarkable method by which shoots destined for climbing reach a wall which will afford them a support is observed in several tropical Bignoniaceæ related to *Bignonia unguis*, one of which, *Bignonia argyro-violacea*, growing by the Rio Negro in Brazil, is represented in fig. 170. This plant bears two kinds of leaves: simple leaves, the blades of which attain to a considerable size, and others which, like the leaves of the vetch (*Lathyrus*), bear two opposite leaflets on one stalk and end in a structure which divides into three limbs with pointed hooked claws, and which is not unlike the foot of a bird of prey.

The development of this clawed, grasping organ always precedes that of the leaflets, so that in the youngest stages the green leaflets only appear as minute scales. Leaves ending in claws are only found on stems which, so to speak, have to seek a firm, safe support for the flowering and fruit-bearing shoots to be developed later on. These stems, however, are thin, much elongated, and are always pushing out new internodes. They hang down as long threads from the tree, whose bark is already quite covered, and which offers no space for a new settlement, and are easily set in motion by the action of the wind. At the end of each thread can be seen two young leaves placed opposite one another, on each of which only the three hooked limbs are at first developed, appearing to be extended for prehensile purposes, just as in a bird of prey. If the shoot oscillating in the air fails to encounter an object which it can seize with its claws, the latter fold back, and the leaflets are developed. Before the following day the filamentous stem has produced a new portion similarly equipped. These fresh claws are again extended, and the supple stem again sways in the wind, in the hope of being able to catch hold of a firm object. The same thing is repeated day after day until some suitable anchorage comes within reach of the elongating shoot. Now is the time for the development of the clamp-roots, which have to fix the stem to the substratum still more firmly than the claws could do. The climbing roots are really already present at each node of the filamentous stem as small protuberances, but they remain quite short until such time as the swaying shoot effects its attachment. Then

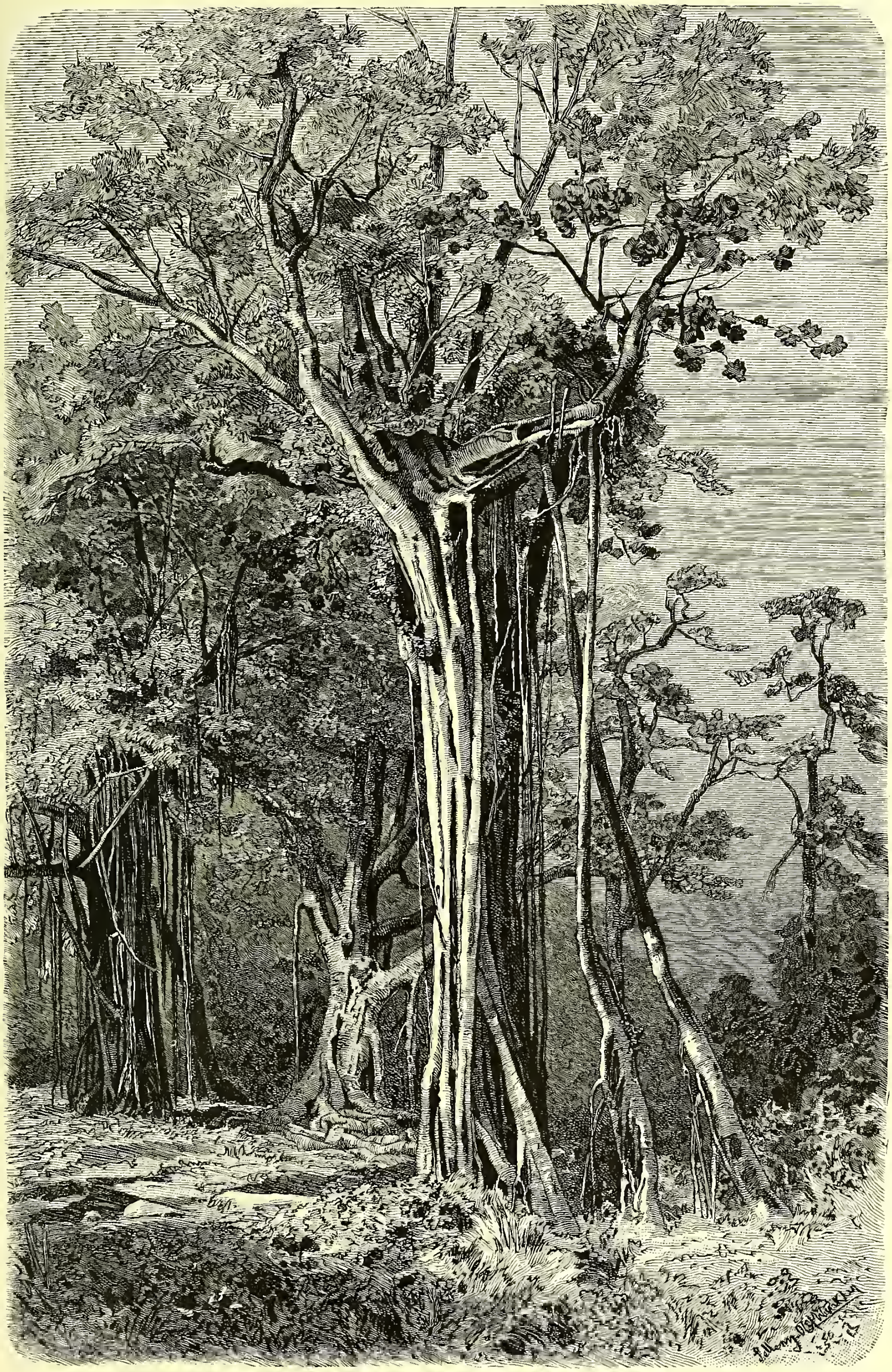

Fig. 169.—*Ficus Benjamina* with incrusting climbing roots. (After a drawing from nature, by Selleny.)

they grow out, elongate, and produce lateral branches, as may be seen in fig. 170. Under favourable conditions, *i.e.* when these swaying shoots reach an unoccupied support and become permanently attached there by their scandent roots, these anchoring shoots exhibit a marked change of habit. They give rise to vigorous and compact shoots with simple leaves destitute of claws, and may unfold flowers and ripen fruit. In due time, when the space has become occupied, pendent shoots are again produced which explore the neighbourhood for a new anchorage in the manner already described.

The group of root-climbers as a whole undoubtedly presents many points of resemblance to forms with stems prostrate on the ground. The climbing stems of Ivy remind one of the stems of Periwinkle, the climbing stems of species of *Pothos* of the creeping stems of the Snake-root (*Calla palustris*), the climbing stems of *Tecoma radicans* of the runners of strawberry plants. The only real difference is that in one case the substratum is the surface of the soil, while in that of climbing stems it is the abruptly-ascending surface of rocks and tree-trunks. And this distinction is wanting in the Ivy. Ivy stems which grow over stony ground, fix on to the horizontal blocks of stone by climbing roots exactly as on vertical walls of rock. If mould is present in the crevices of these stone blocks, the climbing roots become true absorbent roots, not only fastening the stem to its substratum, but also taking up food. But ivy stems climbing up steep rocky walls also behave in this way. The roots which proceed from the portions of the stem growing over the bare stone wall are climbing roots, but as soon as the stem in its growth comes to a crevice filled with earth, the roots developing at that point become absorbent like those which it produces when creeping on the ground.

Thus it is clearly impossible to draw a sharp line between climbing and creeping stems. Similarly, on the other hand, there are some climbing stems transitional between this condition and an erect habit. Ivy, *Tecoma radicans,* the climbing species of *Ficus,* even several tropical aroids, and the Brazilian *Marcgravia umbellata,* exhibit this peculiarity. In the last-named, so soon as it has climbed up a tree-trunk or steep rocky wall into an illuminated place, it alters its growth completely. The shoots now formed up above no longer avoid the light; they no longer develop climbing roots for attachment to the substratum, their wood becomes more extensive, the hard bast surrounding the wood is much more strongly developed, the shoots now not only stand erect without support, but are even able to withstand flexion, and develop flowers with abundant honey and ripe fruits. The erect shoots of Ivy and of the climbing species of *Ficus,* bathed in sunshine, also unfold foliage-leaves, which are strikingly different from those of the climbing shoots in size and shape, and even in their internal structure. Anyone knowing only the long filamentous shoots of *Ficus stipulata,* used for covering the walls in green-houses, happening to see the vigorous shoots of this plant with large leaves and figs, would think it impossible that both should belong to one and the same plant

The erect stems of the Ivy, adorned with cordate shining foliage-leaves when treated as slips or cuttings, send absorbent roots into the ground and ramify; but, strangely enough, the shoots which they develop, although they now spring close upon the ground, do not become climbing stems, but exhibit exactly the same structure, the same erect position, and the same foliage as the shoots on the top of a wall or on the summit of a tree. Anyone seeing for the first time

Fig. 170.—*Bignonia argyro-violacea*, from the banks of the Rio Negro in Brazil.

such Ivy grown in pots, is tempted to mistake it for some erect tropical *Aralia*, and even experienced gardeners and botanists may be misled by these plants. We are involuntarily reminded by these successive shoot-structures, which differ so much in their outer form and internal construction, of the alternation of generations occurring in Vascular Cryptogams, and so much the more since the climbing shoots which precede the erect flowering shoots do not develop flowers and fruits, and thus to some extent resemble an asexual generation.

Several Indian species of fig, the stems of which climb up rocky walls and

adhere to them by girdle-shaped, flattened, and in part lattice-forming roots, send up an erect stem with large foliage when they have reached the top of the wall or the summit of the block of stone. By this time the leaves of the climbing parts of the stem have fallen away. Generally, this climbing stem, the first stage, as it were, can no longer be recognized as such; only the clamp-roots which proceeded from it, which have meanwhile become much thickened and wide-meshed, appear in a most remarkable manner like a lattice-work spread out over the stone. Any one not knowing the history of development of these species of fig, would think that the stems rising erectly from the top of a block of stone or in the cleft of a rocky wall, had germinated in the place where they rise up into the air, and had sent down from thence a net-work of aërial roots enveloping the stone. This idea, which at first occurs to everyone who looks at the two fig-trees faithfully represented on the left-hand side of fig. 171, does not, however, correspond with the actual process of development. The lattice-forming roots adhering to the stone are not sent out by the small trees rising above them, but have been developed by the climbing stem which had mounted up by their help, and then became transformed into an erect stem growing freely up into the air. We must also guard against generalizing and regarding all root-structures of this kind as climbing roots. In the tropics there are plants whose erect stems do send down aërial roots which continually ramify, and then look deceptively like lattice-forming climbing roots.

[For further details as to climbing plants the reader is referred to H. Schenck's masterly *Beiträge zur Biologie und Anatomie der Lianen.* Jena, 1892. Ed.]

ERECT FOLIAGE STEMS.

Plants with procumbent and subterranean stems preponderate in high mountain and in arctic regions, whilst in these places the majority of woody stems cling closely to the substratum, or are embedded in the soil. Lateral shoots rising erect from the ground, of course, often spring from these main stems, but they bear no foliage, or possess green leaves only at the base, and terminate in flowers. They are essentially of the nature of flower-stalks or scapes, and are for the most part to be regarded as floral-stems. The few flowerless, erect foliage-stems which are met with in these frosty districts are all very short, usually closely crowded together into a carpet, or have the form of numerous erect branchlets; they seldom rise more than a span-high from the ground. The only noticeable erect stems besides the type of low, woody shrubs are the culm and the herbaceous stem. On passing from elevated regions down into the valley, and from the arctic zone southwards, besides these forms, we meet with reeds, high shrubs and trees, and still nearer the equator we see the erect stems of cactiform plants, bamboos, and palms.

In this connection the terms *caudex, culm, stalk,* and *trunk* are used to indicate the forms of erect foliage-stems standing out in the landscape, terms

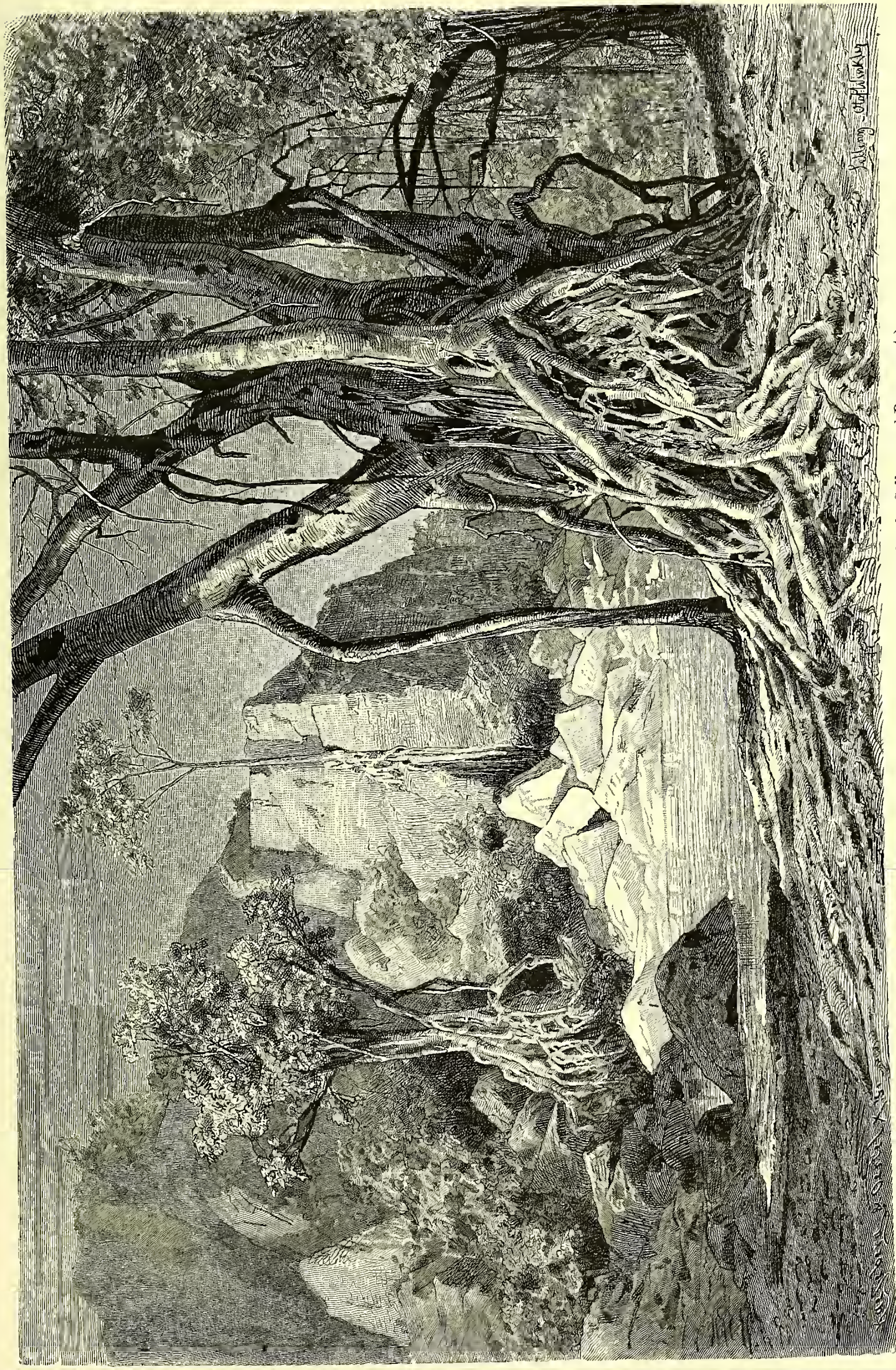

Fig. 171.—*Ficus* with lattice-forming climbing roots. (After sketches by Selleny and Ransonnet.)

which have arisen in the popular tongue, and of which everyone thinks he knows the meaning; these words have also been admitted into scientific terminology, although, when more closely examined, they are seen to be ill-adapted for the nomenclature of erect stems. Thus there are procumbent culms, procumbent caules, and procumbent tree-trunks, and it is therefore not correct to use these terms for erect forms only. It has been proposed to designate the erect stem, which may be compared to a post, a standard-stem (*stirps palaris*), prefixing the word "standard" to the names of the various sorts of erect stem. The names resulting from this combination would prevent any confusion, but, unfortunately, they are cumbrous and unusual, and on the whole unsuited to this book. For these reasons the current expressions will be still employed, with, of course, the proviso that in this case they refer only to standard stems.

The cactiform stem, especially those gigantic specimens which are natives of the Mexican plains, and attain to a height of some 15 metres, might have been taken as a type of a standard-stem. A group of these is represented in Plate VII. on the left. They look like posts which have been driven into the ground to form the foundation for a scaffolding. But since these stems have no foliage-leaves, or rather, since their leaves have been transformed into spines, so that the formation of organic materials, which is usually performed by foliage, has to be done by the green cortex, they cannot really be reckoned as foliage-stems, and can only be mentioned here incidentally.

The *caudex* (*cauloma, caudex*) has the greatest claim of all the series of erect foliage-bearing stems to be compared to a standard. The form seen in slender palms, to which the term *Caudex columnaris* has been applied, stands foremost in this respect. The group of "Palmyra Palms, Ceylon", represented on the accompanying Plate VIII., which is a copy of a large water-colour drawing from nature by Königsbrunn, gives a clear idea of this form of caudex. As a rule, the height of palms is much exaggerated; there is a great temptation, especially in the case of isolated stems, to estimate them as much higher than they really are. This is on account of an optical illusion which comes into play just as in the estimation of the heights of mountains. An isolated mountain peak rising up abruptly is, at first sight, always thought to be higher than a continuous ridge which gradually ascends in gentle slopes, although both may have exactly the same elevation; and the same thing occurs in estimating the height of stems. An isolated Palmyra Palm rising from among low shrubs appears to be much higher than one which is actually taller, but which grows in the midst of a group of trees and whose summit only rises a little above the other tree-crowns. The highest columnar caudex is shown by *Ceroxylon andicola,* a palm growing in the Andes, of which stems are known 57 metres in length. The caudex of the Cocoa-nut Palm (*Cocos nucifera*) attains a height of 32 metres, and that of the Palmyra Palm (*Borassus flabelliformis*), represented in the plate VIII., 30 metres. Most other palms are lower than this, the great majority never exceeding 30 metres. The so-called Dwarf Palm (*Chamærops humilis*) is

PLATE VIII.

PALMYRA PALMS, CEYLON.

Printed from the originals by the BIBLIOGRAPHISCHES INSTITUT, Leipzig.

Fig. 172.—Bamboos in Java. (From a photograph.)

only 4 metres high, and there even exist palms whose caudex barely rises above the ground.

The caudex of tree-ferns and cycads also remains comparatively short. When travellers speak of the gigantic trunks of tree-ferns, they only mean gigantic in comparison with the stems of the ferns growing in our European forests, which either never appear above the ground, or like those of the ostrich fern (*Struthiopteris germanica*), only 10 cm. above the soil. The New Zealand tree-fern *Dicksonia antarctica*, with a diameter of 40 cm. reaches a height of 15 metres, and the caudex of *Alsophila excelsa*, with a thickness of 60 cm., is 22 metres high. The cycads scarcely ever reach this height, nor do the various other flowering plants possessing a caudex, such as the species of the genera *Yucca, Dracæna, Urania, Pandanus, Aloë,* and *Xanthorrhœa.* The celebrated Dragon-tree (*Dracæna Draco*) of Orotava, whose age is estimated to be 6000 years, has a circumference of 14, and a height of 22 metres.

The caudex is in most cases simple, but several Pandaneæ and dragon-trees, and among the palms, the Doum Palm (*Hyphæne thebaica*) growing in the Nile valley and *Hyphæne coriacea*, fork and develop a few short branches when their main caudex has attained a great age. Many caudices, *e.g.* those of the tree-ferns *Dicksonia antarctica* and *Todea barbata* are completely covered with short aërial roots, in consequence of which their surface has a peculiar bristling appearance. Many caudices are also abundantly provided with thorns. For the appearance of most of them it is of importance whether the dead leaves break off above the base, so that the leaf-sheaths persist, or whether the leaf-sheaths are detached with them, only a scar being left on the caudex. In the former case the stem is clothed sometimes with ridges or scales, sometimes with a fibrous integument, or even with dry stumps. In the latter case it is covered with circular or shield-like scars. The caudex of *Caryota* (*cf.* fig. 74, p. 311) becomes quite smooth after the leaves have fallen off, and looks like a gigantic culm; indeed, it forms a link between the caudex and that kind of stem which is termed a culm.

The stem-structures which are comprehended under the name *culm* (*culmus*) differ in size even more than does the caudex. They may be classified in the following groups, which, of course, are not sharply marked off from one another. First, the *culm* in the narrow sense of the word, which embraces those forms whose stem does not exceed a diameter of ½ cm.; then the *reed*, which is not branched, whose internodes are always surrounded by long sheaths, and whose stem has a diameter of ½–5 cm.; and, further, the *bamboo*, which divides into numerous branches, having short leaf-sheaths and a very peculiar anatomical structure; this will again be referred to in the next chapter. The culm exhibits its highest proportions in bamboos, especially in the species represented in fig. 172, which attains to a height of 25 metres and a thickness of more than half a metre. From this extreme, on the one hand, to the delicate little culm 2–3 cm. long, of many annual grasses of the Mediterranean flora, there exists an unbroken series about the middle of which comes the Southern Reed (*Arundo Donax*) with a height of 4 m. and a diameter of 5 cm.

The *stalk* (*caulis*) does not become woody, but remains green; it persists only for a single period of vegetation, and then dies down. The stem of annual and biennial plants classed as herbs (*herbæ*) is called a "herbaceous" stem (*caulis herbaceus*), and that of perennial plants a "suffruticose" stem (*caulis suffruticosus*). By the term "undershrub" (*suffrutex*) we understand especially those perennial plants whose underground stem annually sends up shoots which do not become woody, but which die off at the beginning of the winter, *e.g.* the Dwarf Elder (*Sambucus ebulus*), the common Avens (*Geum urbanum*), and the Meadow Sage (*Salvia pratensis*). Whilst the caudex and culm are generally circular in cross-section, the caulis is usually 3-, 4-, and 5-ribbed. Longitudinal furrows traverse its exterior, and the relation of these to the nearest leaves will be described more in detail subsequently. The extreme limits of size of the caulis have already been discussed on p. 656.

The *woody stem* (*truncus*) either remains without branches until it has attained a considerable height, when it is called "arborescent" (*truncus arborescens*), or it is very short, and its branches spring from near the ground, in which case it is called "shrubby" (*truncus frutescens*). A distinction is also drawn in descriptive botany with regard to size between the "tree" (*arbor*) in the narrower sense, and the "small tree" (*arbuscula*), the "shrub" (*frutex*) and the "small shrub" (*fruticulus*). The expression "semi-shrub" (*semifrutex*) may be employed to denote shrubs whose yearly shoots only become woody at the base before the next period of vegetation, and which wither and die off above this. These form a transition to the undershrubs mentioned above.

Of all these forms of woody stem the tree, especially prominent on account of its mass, naturally claims most interest. Nor is this interest limited to the botanist; it is shared with him by the landscape-painter, forester, gardener, indeed, by every lover of nature, each from his own particular point of view. Among all the forms of vegetation trees are the best known; they have received a special name in all languages, different nations have chosen certain species of their country as favourites, and have extolled them as national trees in their songs, and even in the religious observances and customs of ancient and modern times trees played and yet play a prominent part. Many persons who have never occupied themselves with botany, and have never observed plants closely, but who have a strongly-developed sense of form, are able to distinguish and recognize the various kinds of trees at the first glance and at considerable distances. How is this possible? The explanation is very simple. The aspect of every tree, like the face of every man, presents certain features which are peculiar to it alone; these features imprint themselves almost unconsciously on the memory of anyone who is occupied much in the open, and the species is recognized again by him, even at a distance, like an old friend one meets in the street. To the landscape-painter these features, which, taken together, form what has been termed the habit of the tree, are particularly important, for he has to seize them and give them artistic expression. Our task here, however, is to detail and to interpret these features in the appearance of the trees, or let us put it, to give a scientific basis to the "habit".

Fig. 173.—The Oak.

Fig. 174.—The Silver Fir.

The limits of this book do not allow me to treat this theme as fully as my inclination and predilection for the relations between art and science would prompt me to do, but as a tree may be sketched on a wall with a few strokes, so I will endeavour to represent the principles of the "habit" in a few words.

In every tree the position of the buds depends upon the position of the foliage-leaves, and it is evident that the distribution of the lateral twigs proceeding from a branch is also dependent upon the position of the leaves. The correlation between the arrangements of leaves and of branches is therefore the first which has to be considered in explaining the "habit". Like leaves, the branches are either whorled or decussate, or arranged along a spiral line, and it may therefore be said that the branches also exhibit the definite geometrical relations which were described in detail for leaves on pp. 396–407; even this fact gives a characteristic stamp to every tree. How very different are maples and ashes with their decussating branches, in comparison with elms, limes, and alders, with leaves arranged on the one-half and one-third system, and with beeches, oaks, and poplars characterized by the two-fifths and three-eighths arrangement; they differ not only in detail, but also in the grosser features of the whole tree-crown. Not only are the bare trees in winter-time readily recognizable at a distance by their ramification, but every portion of the leafy crown derives its particular contour in consequence of this branching. Then, again, the size and shape of the foliage-leaves have to be considered in interpreting the habit. This does not imply that the painter should represent the individual leaves, so that they could be recognized, for that would in a picture be undesirable. The significance of the configuration of the single leaves lies rather in the fact that they regulate the form of the whole tree. The boughs and branches of trees with narrow, linear, or needle-shaped leaves have far less to support than those which are adorned with large, flat, extended leaf-blades. Trees of the former class are characterized by their height, of the latter by their width, a difference which appears in the trees of all parts of the world. For example, the difference in the architecture of slender, narrow-leaved eucalyptuses and willows, and the broad-leaved paulownias, catalpas, and planes, with their wide-spreading boughs, is very striking. If we compare the illustrations of oak and fir placed opposite one another on the preceding pages, we notice that the needle-bearing boughs and branches borne by the slender stems of the fir-tree scarcely occupy a third of the space of that taken up by the thick, heavy trunk of the oak, the leaves of which are so much broader.

A third point which comes under consideration is the light required by the leaves on the lower boughs of older trees. The thicker and more abundant the foliage on the summit or top of the crown, the deeper becomes the shade around the lower part of the main trunk. If the lower boughs are not able to elongate continually by means of new additions they die, together with their shaded foliage, withering up and breaking off either wholly or in part at the first opportunity and falling to the ground; but if they have this capacity of elongating, they push and extend their leafy branches as far as possible out of the circle of the shadow into the

sunlight, and frequently curve up towards the light, as may be well seen in ash and chestnut-trees, and also in the spruce firs represented on p. 415.

The lower portion of the stem which has lost its boughs increases in circumference as the burden it has to bear becomes greater, and its thickness and strength in every species bears a definite relation to the weight of the crown. The increase of circumference is brought about by the addition each year of new masses of wood to those already present. In very young stems the wood appears in the form of strands, symmetrically arranged round the central pith, closely adjoining one another and forming a cylinder which is only interrupted by the medullary rays. The annual increments of wood, deposited on the periphery of this primary ring, also have the form of rings in cross section; each is known as an *annual ring*. The age of a felled tree can be reckoned from the number of these annual rings, and obviously the girth of the stem increases with their increasing number. The enlargement of the circumference is, however, not without its effect on the external appearance of the stem. While still quite young, the stem possesses a covering skin (epidermis) which closely surrounds the green tissue of the cortex. This epidermis, however, only keeps pace with the development of the interior of the stem as long as this particular part continues to grow in length. When it stops, and increase in thickness commences, the first skin perishes, and is replaced by a second, the so-called *periderm*. This usually begins to develop even at the end of the first period of vegetation. The most important constituent of periderm is cork, a tissue of cells impervious to water and almost impervious to air, and therefore excellently fitted as a covering for the inner sap-conducting portions of the stem. Whatever lies outside this cork, or is secreted through it from the inner sap-containing portions, dries up and dies. If the periderm is developed immediately beneath the epidermis, this alone perishes; but if the periderm arises in the deeper layers of the cortex, a considerable thickness of cortex also dies and remains outside the cork as a dead dry crust. This inner periderm with the dead adhering parts of the cortex is called the *bark*.

The development of the periderm keeps pace with the development of the stem. As soon as the wood of the stem becomes thicker, by the intercalation of a new annual ring, the mantle of periderm stretches, and consequently the whole envelope of bark. In many trees this bark remains year after year on the periphery of the stem; it becomes fissured by the continuous increase in thickness, but new bark is as continuously produced from within closing up the fissures. In other instances a part of the bark falls off on to the ground in consequence of the thickening of the stem, and is again replaced by new bark from within.

Since every kind of tree has its own special bark, the texture and colour of this structure contributes not a little to the appearance of the whole tree; it forms one of the characteristic features which must not be overlooked when describing the habit of the tree. The following are the most important forms of bark. First the *scale* bark, which is detached annually in the form of shields and plates, to be seen especially well in the stems of planes, almond willows,

and many species of Australian eucalyptus. Then the *membraneous* bark, which separates as dry films and ribbons; this form of bark is shown in the Common Birch (*Betula alba*), illustrated opposite. Many species of the Australian genus *Melaleuca* exhibit a bark which, when stripped from the stem, looks deceptively like a thin silky material. A third form is the *ringed* bark, which is detached from the stem in the form of thin, irregularly-fissured tubes, and is especially developed in the Mock Orange (*Philadelphus*). A fourth form, of which the Vine (*Vitis vinifera*) may serve as an example, is the *fibrous* bark which is detached as numerous stiff threads. Finally there is the *fissured* bark, which is produced on the stems of the oak, lime, ash, and numerous other leafy trees. In this form the bark is not detached in large pieces, but is ruptured by the increasing thickness of the stem, causing longitudinal fissures with a sinuous or zigzag course, by which in one case only narrow ridges and grooves, and in other cases broad angular patches are outlined. Epiphytes, especially mosses and lichens, prefer to settle on fissured bark, and older stems with this kind of bark are in temperate regions usually overgrown with cushions of moss, in the tropics with ferns, bromeliads, and orchids. Such a colonization would be impossible in bark which falls off annually, and the stems of plane trees are not only free from epiphytes, but always look as if they had been scraped or peeled.

The form of the bark is so characteristic that by it alone the species of the tree can be recognized; it therefore constitutes an important feature in the picture of a tree, nor can it be altered according to fancy. It is inadmissible that artists should combine the studies they have made of various trees as they please, perhaps putting the crown of an oak on the trunk of a plane. That the colour of the bark is as important in the habit as the tint of the foliage goes without saying, and it is evident that the relative sizes of the various trees round about must also be considered.

The height and age of trees cannot be represented in definite figures, but this much is certain, that every species of tree, just like every species of animal, is limited to a certain size and age which is but rarely exceeded. The records of age which have come down to us are for the most part too great. When trees of primeval forests are said to be a thousand years old, the estimates are based upon conjecture, and only in rare cases on actual measurements. The celebrated Baobab (*Adansonia digitata*) was reckoned by Adanson on the ground of the thickness of the annual growth to be about 5000 years old, but whether a miscalculation has not crept in must remain uncertain. The age of the celebrated Dragon Tree of Orotava, already mentioned once before, has even been estimated at 6000 years; the Plane of Bujukdere, on the Bosphorus, at 4000; and the so-called Mexican Cedar (*Taxodium Mexicanum*) was estimated by Humboldt at 4000 years. I would not like to stand security for these numbers either. On the other hand, the following extreme limits of age are calculated with fair accuracy:—For the Cypress (*Cupressus fastigiata*), 3000 years; the Yew (*Taxus baccata*), 3000; the Chestnut (*Castanea vulgaris*), 2000, the Oak (*Quercus pedunculata*), 2000; the

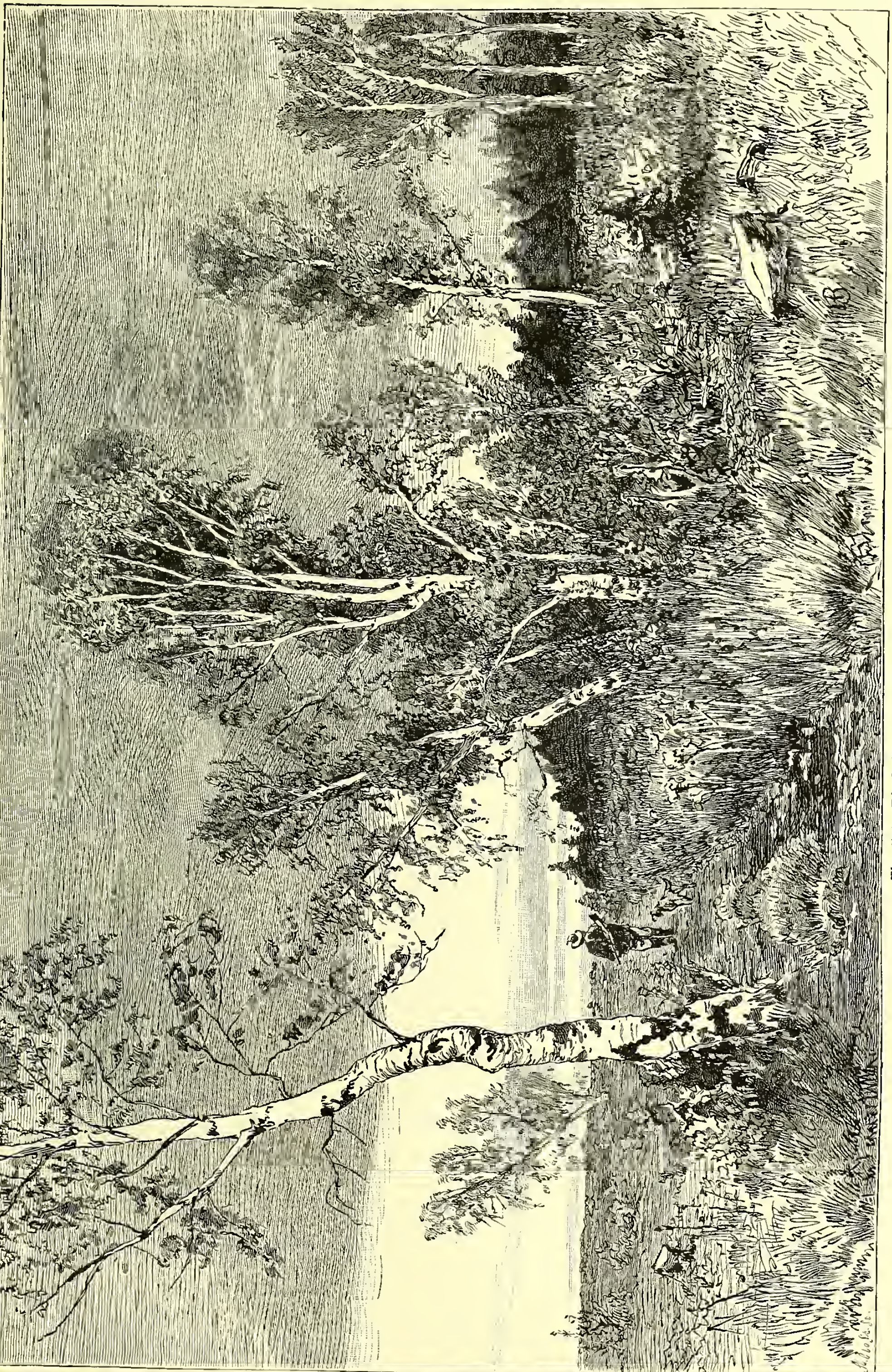

Fig. 175.—Birch Trunks with white membraneous bark.

Cedar of Lebanon (*Cedrus Libani*), 2000; the Spruce Fir (*Abies excelsa*), 1200; the Broad-leaved Lime (*Tilia grandifolia*), 1000; the Arolla Pine (*Pinus Cembra*), 500–700; the Larch (*Larix Europæa*), 600; the Scotch Pine (*Pinus sylvestris*), 570; the Abele (*Populus alba*), 500; the Beech (*Fagus sylvatica*), 300; the Ash (*Fraxinus excelsior*), 200–300; the Hornbeam (*Carpinus Betulus*), 150 years.

The certified estimates of the heights of trees are of such general interest that they are included below in the following table:—

Name.	Height in metres.	Name.	Height in metres.
Peppermint Tree (*Eucalyptus amygdalina*)	140–152.	Mexican Cedar (*Taxodium Mexicanum*)	38·7.
Mammoth Tree (*Sequoia gigantea*)	79–142.	Durmast (*Quercus sessiliflora*)	35.
Silver Fir (*Abies pectinata*)	75.	Plane (*Platanus Orientalis*)	30.
Spruce Fir (*Abies excelsa*)	60.	Ash (*Fraxinus excelsior*)	30.
Larch (*Larix Europæa*)	53·7.	Baobab (*Adansonia digitata*)	23·1.
Cypress (*Cupressus fastigiata*)	52.	Arolla Pine (*Pinus Cembra*)	22·7.
Scotch Pine (*Pinus sylvestris*)	48.	Tree of Heaven (*Ailanthus glandulosa*)	22.
Beech (*Fagus sylvatica*)	44.	Oak (*Quercus pedunculata*)	20.
Cedar of Lebanon (*Cedrus Libani*)	40.	Hornbeam (*Carpinus Betulus*)	20.
Abele (*Populus alba*)	40.	Yew (*Taxus baccata*)	15.

Eucalyptus amygdalina (represented in fig. 176, after a drawing by Selleny), consequently attains the greatest height of all known trees. The highest of these stems placed beside St. Paul's Cathedral would tower about 40 metres above the cross, and would be only 4 metres lower than Cologne Cathedral.

That the height and girth of trees do not increase proportionately will be seen by comparing the following table with the previous one:—

Name.	Diameter of trunk in metres.	Name.	Diameter of trunk in metres.
Chestnut (*Castanea vulgaris*)	20.	Cypress (*Cupressus fastigiata*)	3·2.
Mexican Cedar (*Taxodium Mexicanum*)	16·5.	Elm (*Ulmus campestris*)	3.
Plane (*Platanus Orientalis*)	15·4.	Silver Fir (*Abies pectinata*)	3.
Deciduous Cypress (*Taxodium distichum*)	11·9.	Abele (*Populus alba*)	2·8.
Mammoth Tree (*Sequoia gigantea*)	11.	Beech (*Fagus sylvatica*)	2.
Baobab (*Adansonia digitata*)	9·5.	Spruce Fir (*Abies excelsa*)	2.
Broad-leaved Lime (*Tilia grandifolia*)	9.	Arolla Pine (*Pinus Cembra*)	1·7.
Peppermint Tree (*Eucalyptus amygdalina*)	8.	Ash (*Fraxinus excelsior*)	1·7.
Oak (*Quercus pedunculata*)	7.	Larch (*Larix Europæa*)	1·6.
Yew (*Taxus baccata*)	4·9.	Cornel (*Cornus mas*)	1·4.
Oak (*Quercus sessiliflora*)	4·2.	Scotch Pine (*Pinus sylvestris*)	1.
		Hornbeam (*Carpinus Betulus*)	1.
		Tree of Heaven (*Ailanthus glandulosa*)	0·9.

According to these certified estimates there actually exist plants whose stems attain a diameter of 20 metres, and others whose stems rise to a height of 152 metres above the ground.

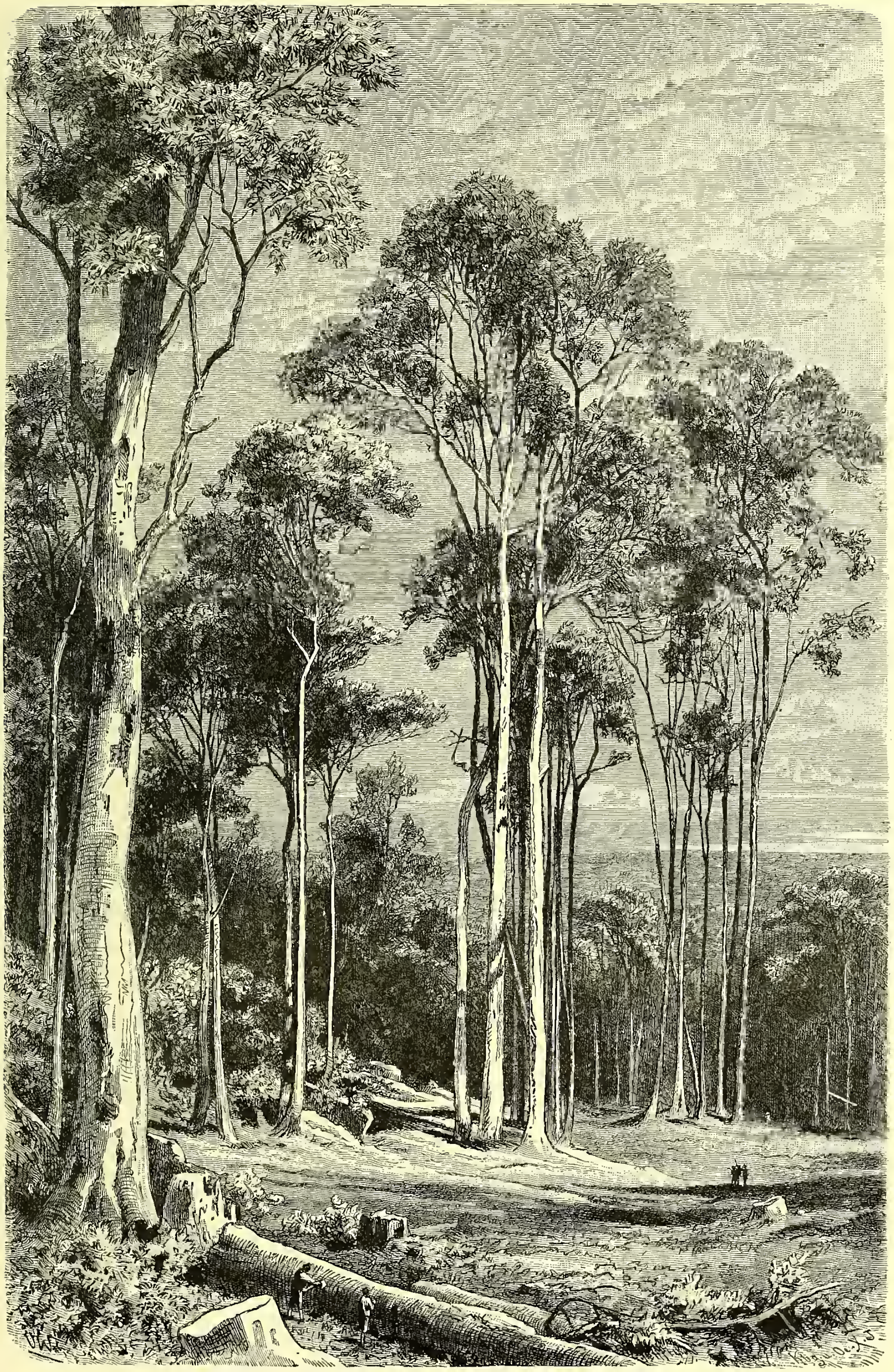

Fig. 176.—Eucalyptus trees in Australia. (After a drawing by Selleny.)

RESISTANCE OF FOLIAGE-STEMS TO STRAIN, PRESSURE, AND BENDING.

When the weight of the individual parts of these huge trees is considered, it is difficult to understand how their comparatively slender main stems are able to support a crown weighing many thousand kilogrammes, and how it is that the boughs extending far out from the trunk horizontally do not crack and break under the weight of the branches and leaves they carry. The culms of grasses and the stems of bushes and herbs are also so loaded as to astonish us, and we cannot help asking how it is they are able to keep erect, and how, when their equilibrium is disturbed, they can resume their normal resting position almost at once. If we wish to investigate the mechanisms which make it possible for these plants to maintain their stems in this position without assistance, we must in the first place consider the lowest portion of the erect main stem, since it is that part which would naturally have the heaviest burden to carry. Given that the pressure caused by the loading operates in the direction of the axis, the main stem must exhibit contrivances enabling it to resist the vertical pressure; in other words, it must possess what is known as columnar strength. With the exception of some palms whose erect stems rise up like pillars from the ground, and whose leaves project equally in all directions, such a pressure, acting exactly in the direction of the axis of the stem, is but rarely found. As a rule some inequality in the stem or crown, although perhaps but slight, causes the pressure to be diverted from the central axis; the stem is bent by the one-sided burden, and has need not only of columnar strength, but of resistance to flexion as well. Winds also will effect a bending, not only by direct impact, but also inasmuch as they displace the centre of gravity of the load sustained by the lower part of the stem. Observation shows us that this bending is only rarely followed by the fracture of the stem. Not only grasses and reed culms, but also the thinner erect branches of trees, shrubs, and bushes, and even palm caudices may be bent down a considerable distance, but, when the wind subsides, quickly return to their erect position without having suffered the least harm.

Formerly but little attention was given to these phenomena, perhaps because they were so common and frequent, or perhaps because it was thought to be impossible to give a scientific explanation and reason for the swaying of branches in the wind. It was reserved for modern times to explain the mechanisms underlying the returning of bent stems to a definite position of rest, and the contrivances which permit such stems to bend but not break, even when considerably loaded and under strong pressure. Investigations into this subject have demonstrated that the bearing capacity and power of resisting bending moment in plant stems are obtained by structures exactly similar to those used by man in spanning a river with bridges, in fixing the supports of a roof, of wooden partitions, &c. Further that the principle so important to every builder, the obtaining of the greatest strength possible with the smallest outlay

of material, also finds expression in the construction of the stem. In one case we are reminded of the system of tubular bridges, in other cases of that of lattice-bridges; here of a massive pillar-like structure with architrave and flattened top, there of a Gothic building with pointed arches, buttresses, and steep gables; but the special conditions of the habitat are always taken into consideration, and the whole structure for this reason always exhibits the greatest adaptability of the means to the end.

The framework which gives the desired strength to the whole structure is made up of parts which would be called by builders "constructive pieces", and these are in turn made up of special cells, termed mechanical cells. *Mechanical cells* have already been alluded to in the description of the conducting-apparatus (*cf.* p. 474), although only very briefly. It was pointed out that the tubes and cells which serve for the transport of fluid materials up and down the plant are usually united into a bundle, the so-called vascular or conducting bundle, and that when the constituent parts of this bundle occur in organs which are exposed to the danger of being broken, mechanical cells always make their appearance alongside the conducting cells and vessels. The delicate vascular bundles then usually lie embedded in a channel of hard bast, or are protected laterally by a strand of hard bast, or more rarely they are interposed between two bands of this tissue. These strands and bands of hard bast are frequently of merely local importance for the vascular bundle, and may be likened to the strengthening appliances of gas and water-pipes in human dwellings, which are very important in their special use, but do not help to strengthen the whole house. Very often, however, these special supporting agents of vascular bundles are absent, and then the conducting tissues are affixed to the groups of mechanical cells which form the foundation-framework of the whole structure.

The *hard bast* is the mechanical tissue most often employed in both cases. To the naked eye the cells of hard bast look like tiny threads. They are elongated, fusiform, pointed at both ends, and interlaced and dovetailed with one another as shown in fig. 125 [5] (p. 469). They are generally about 1–2 mm. long, but in certain cases attain a much greater length; those of the Hemp are 10, those of Flax 20–40, of the Nettle 77, and of *Boehmeria nivea* even 220 mm. long. The walls of hard bast cells are always very much thickened, and the cell-cavity is very narrow, often being reduced to an exceedingly fine canal, in some cases, *e.g.* in the cells of hard bast of *Corchorus olitorius* (known as Jute), the canal here and there is quite obliterated, so that the cell is transformed into a solid fibre. It is concluded from the direction of pores which sometimes appear in the walls that the micellæ which build up the walls of these thick bast-cells are arranged in left-handed spiral lines, and this spiral torsion is supposed to be connected with the strength of the whole hard bast cell. It is known that bundles of straight threads are not as strong as bundles twisted into a string, and we are justified in supposing that this is also the case with the rows of micellæ forming the extremely fine fibrillæ in the walls of the hard bast cell. When a cell of hard bast is fully developed, the living proto-

plasm disappears from its interior, and the narrow space of the cell-cavity becomes filled with air, or less often with a watery fluid. The cell can then no longer continue its growth, neither can it serve to take up and conduct food nor to manufacture organic compounds; it cannot be employed in transformations and transmission of materials, and has exclusively an architectural significance. It is excellently adapted, however, to the task thus assigned to it. Its strength and elasticity are indeed extraordinary. It has been estimated that the bearing capacity of hard bast amounts to between 15 and 20 kg. to the sq. mm. in cross section, and is therefore equal to that of wrought iron; indeed the bearing capacity of many species of plants is even equal to that of steel. Hard bast has this advantage over iron, that it is far more extensible and consequently less subject to breaking. From the consideration of all these properties it becomes evident why the hard bast of many plants has been used by man to such advantage in the manufacture of fabrics, string, ropes, and the like, since very remote times.

Woody fibres, also known as *libriform cells*, differ very little from hard bast cells. Whilst hard bast forms one of the most important constituents of the cortex, the woody fibres form an essential element in the wood of those stems which annually add a new layer to the already existing wood, thus increasing in circumference and exhibiting annual rings in cross section. Their length varies between 0·3 and 1·3 mm., so that they are somewhat shorter than the fibres of the bast. Their walls are as a rule strongly lignified, but in other respects it is impossible to draw a sharp line between the two forms of cells. When a woody stem has grown in thickness and has developed bark on its periphery, the rôle played by the hard bast in the cortex is evidently at an end; the woody fibres then assume the tasks which in the young shoots are allotted to the hard bast, and they might therefore be called the hard bast cells of the wood.

In many plants a special form of mechanical cell-tissue is developed, known as *collenchyma*. The cells which compose it are elongated and connected with one another just like hard bast cells, but they differ from these and from the woody fibres in the fact that their walls are unequally thickened. Where three or four of these cells adjoin one another by their long sides the walls are very thick, but in places the wall common to two neighbouring cells remains thin; the whole of the tissue may be compared to a building in which thick main walls alternate with thin partitions which are strengthened here and there with quartering, and attain a great supporting capacity. A further distinction from hard bast cells and woody fibres consists in the fact that living protoplasm remains in the interior of collenchymatous cells in which chlorophyll-corpuscles are often embedded; moreover, this protoplasm can draw some of the materials necessary for growth through the thin places in the walls from the surronding tissue, and can employ these as building materials;—in a word, the collenchyma is capable of further growth. This explains the advantage of collenchyma over hard bast cells, and woody fibres or libriform cells. The hard bast and libriform cells when once fully formed lose their capacity of further development, and would therefore be of little use as

architectural elements in a still growing portion of the stem; they would either prevent the lengthening of the other tissues, or would be ruptured by the force of the elongating cells, and in both instances would be injurious. The collenchymatous cells, on the contrary, are able to continue developing, they can elongate and grow with the other tissues, and may be compared with the scaffolding of a several-storied building, which is constantly being raised as the work progresses. The collenchyma, of course, has this disadvantage when compared with the hard bast and libriform fibres, that its absolute strength is somewhat less; its bearing capacity is only 10–12 kg. to the sq. mm. in cross-section. The limits of elasticity of the collenchyma are also considerably less, but where hard bast or libriform cells would be unsuitable, from the reasons stated above, collenchyma replaces it. It cannot be said that hard bast and libriform fibres are more important than collenchyma; each in its own way has an especial architectural value, and sometimes the one, sometimes the other, is the more advantageous.

The *hard bast, libriform cells,* and *collenchyma* which are comprehended under the common term *mechanical tissue* are usually arranged in strands running parallel to the long axis of the stem. If they were confined to the centre it would be anything but a suitable arrangement, for an erect stem; they would contribute almost nothing to the resistance to flexion as will be seen from the following considerations. Let us imagine a horizontal, cylindrical stem resting on solid supports at either end and loaded in the middle; it will bend downwards in proportion to the load laid on it, and in doing so the concave side will be shortened and the convex side lengthened; the shortened side will be subjected to compression and the elongated side to tension. These forces will be greatest at the periphery, on the upper and under limiting surfaces, of the bent stem. The opposed forces diminish towards the middle of the stem, and completely vanish at the centre, therefore, in order that the stem should resist bending as much as possible, it is obvious that the strengthening material is best applied when wholly used in the form of flat plates where the forces are greatest. These particular constructive pieces are known technically as *flanges,* and a flange is fixed at either side of a beam which requires to be strengthened against flexion. The mass lying between the two flanges is called the *web,* and the whole beam so constructed is termed a *girder.* Fig. 177 [1] gives a diagrammatic representation of such a girder in cross-section. The web may be composed of much softer material than the flanges; it may consist of a lattice- or merely of a frame-work. Where these girders are developed in plants, the web consists of vascular bundles or of parenchymatous cells, while the flanges are always built up of mechanical tissue. In flat, extended foliage-leaves the girders are fitted in so that their flanges are parallel to the upper and lower surfaces of the leaf, but these leaves only resist bending in one plane. This construction, which can be seen in the leaf-sections given in figs. 86 [1] and 87 [3] (pp. 342–343), would be ill-adapted to stems. An erect stem which is struck by the wind, sometimes from one side and sometimes from another, must be strengthened indifferently on every side, and in accordance

with this demand the most different kinds of combinations of girders are seen developed in it. Usually several, at least two, but often very many girders are so combined that they traverse the axis in common, as shown in the diagrammatic cross-sections in figs. 177 [2, 3, 4]. In this case all the flanges are on the periphery of the stem, and every pair—diametrically opposite one another—must be regarded as belonging to the same girder. In many stems all the flanges have a parallel course; in other cases they are bent in and out, and so connected together as to form a lattice-work of the most complicated kind. In other cases

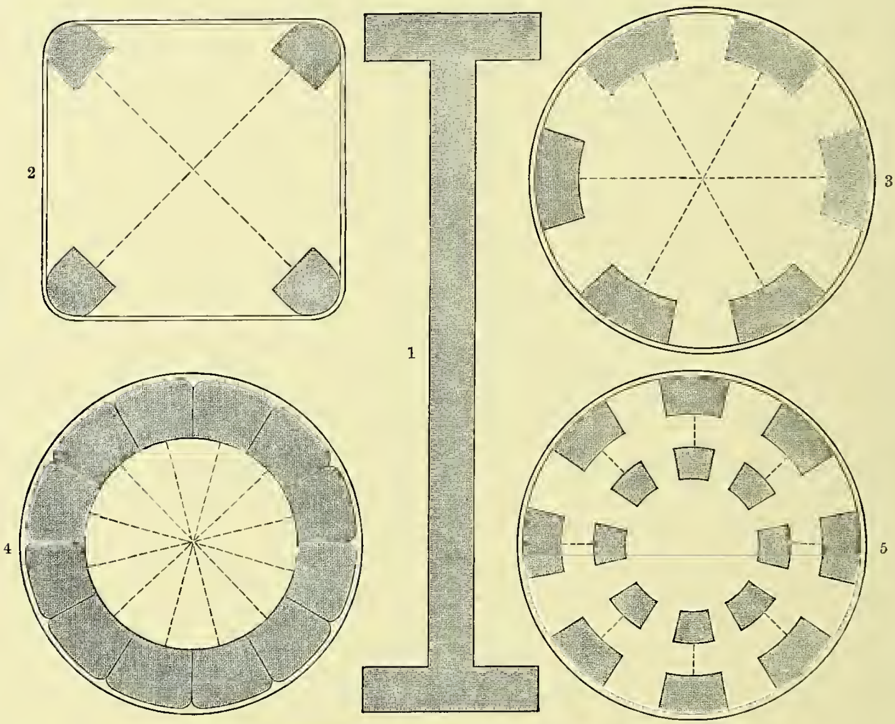

Fig. 177.—Diagrammatic representation of various combined girders.

[1] A simple I (or double T) girder. [2] Two combined girders, arranged crosswise. [3] Three combined girders. [4] Six combined girders; the flanges are laterally in contact to form a cylindrical tube. [5] Four combined girders; their flanges are formed of secondary girders. In Figs. [2–4] the web of the girders is indicated by dotted lines.

all the flanges lying near the periphery of the stem are fused together (fig. 177 [4]) so as to form a cylindrical tube, in which case the web is not required and the stem is either hollow inside, or is filled only with a loose pith. Sometimes each separate flange is itself transformed into a girder, and in this way the flanges of the chief girder become secondary girders, as represented in fig. 177 [5]. There is almost as great a variety in this matter as there is in the arrangement of the strands of leaves, but since researches into the course and grouping of the strands of mechanical tissue in stems are still not far enough advanced for us to be able to place the various forms in well-arranged series, we must content ourselves with sketching the most noticeable cases.

First we will give a general idea of the distribution of mechanical tissue, in as far as it enables erect stems to resist bending. We can distinguish three groups of forms in this respect. The first group includes forms with simple girders whose flanges of hard bast are placed as near the periphery as possible, but are not fused together into a cylindrical tube. The line connecting every pair of flanges passes through the axis of the stem. To this group belong almost all young stems of woody plants, *e.g.* those of willows, oaks, elms, maples, and limes (*cf.* fig. 178 [1]). Special emphasis must be laid on the words "young stems", since in the older stems of these trees—when the wood has become thickened—the hard bast on the outer side of the cambium-ring, and therefore outside the vascular bundle, has finished its task, and its functions are transferred to the wood, more especially to the woody fibres (libriform cells) (*cf.* p. 726).

In the erect stems of undershrubs belonging to this group the simple girders are

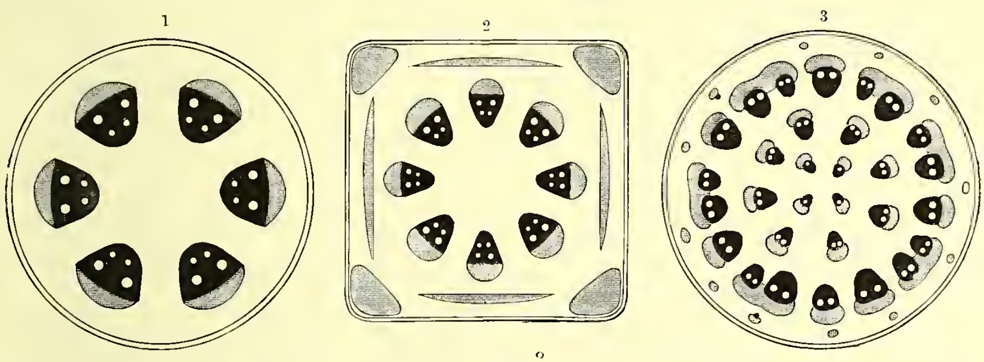

Fig. 178.—Transverse sections of erect foliage-stems with simple girders not fused together into a tube.

[1] One-year-old branch of the Broad-leaved Lime (*Tilia grandifolia*). [2] White Dead-nettle (*Lamium album*). [3] Date Palm (*Phœnix dactylifera*). In these diagrammatic figures the mechanical tissue is grey and the vascular bundles black with white spots.

very often assisted by collenchymatous strands which lie close to the periphery of the stem, and are arranged so that each strand appears to strengthen the bundle of hard bast forming a flange. Fig. 178 [2] shows a transverse section of a stem of an undershrub belonging to this group, the White Dead-nettle (*Lamium album*), in which the further peculiarity is noticeable, that the strengthening, collenchymatous strands in the corners of the four-sided stem are thick and pillar-like, while those at the sides of the stem are broad and flattened. This condition is not an uncommon one. In palms, of which the diagrammatic cross section of the Date Palm (*Phœnix dactylifera*, fig. 178 [3]) may serve as a type, the strands accessory to the simple girders are in the form of numerous bundles of hard bast developed on the periphery of the stem, but not exactly in front of the flanges of the girders. These bundles of hard bast are always in pairs opposite one another, and may be regarded as the flanges of special girders. In these cases the number of girders is always very large, and the flanges appear in two, three, or even more circles in a cross section of the stem. Sometimes also two or three adjoining flanges are fused

laterally with one another, and form what may be regarded as a link connecting this with the following group.

The second group comprises all stems in which the flanges of numerous simple girders are fused laterally so as to form a cylindrical tube. This tube lies as near to the periphery as possible, and consists of hard bast developed from the bast portions of the originally distinct vascular bundles. In consequence of this the vascular bundle is always in connection with the hard bast tube. The various methods of connection, and the presence or absence of accessories to this bast tube

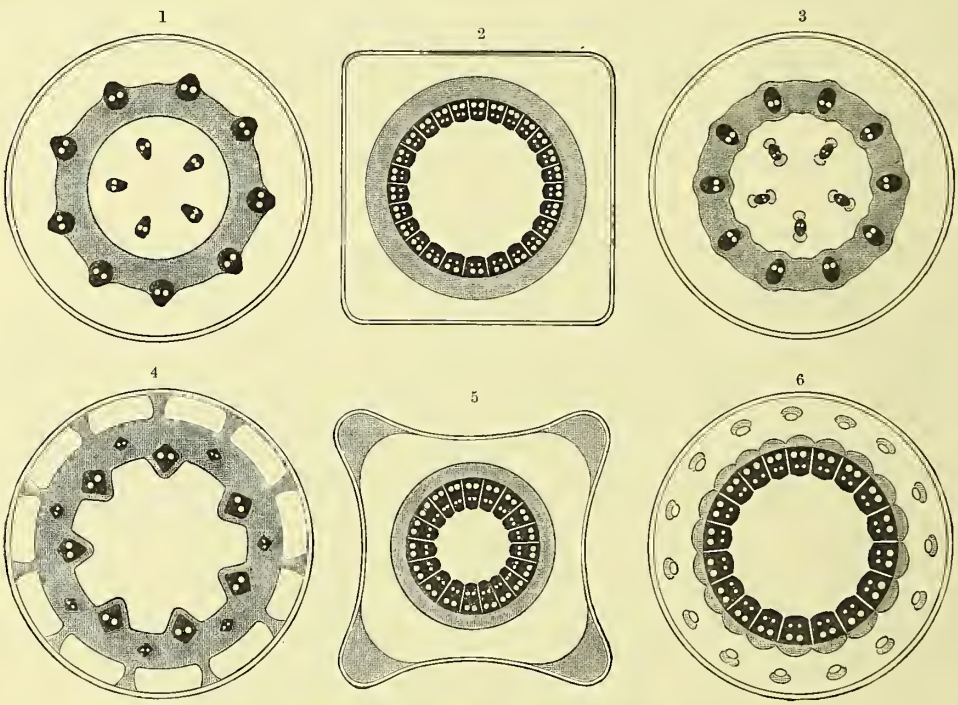

Fig. 179.—Transverse sections of erect foliage-stems with simple girders fused into cylindrical tubes.

1 Crow Garlic (*Allium vineale*). 2 Carnation (*Dianthus Caryophyllus*). 3 *Polygonatum verticillatum*. 4 Purple Molinia (*Molinia cœrulea*. 5 Woodruff (*Asperula odorata*). 6 Sumbul (*Euryangium Sumbul*). In these diagrams the mechanical tissue is represented grey, and the vascular bundles black with white spots.

in its resistance to flexion, give rise in this group to a great multiplicity of structure. Some of the most interesting forms are represented in fig. 179. In fig. 179², the cross section of the stem of a Carnation (*Dianthus Caryophyllus*), the vascular bundles are situated on the inner side of the bast ring; in fig. 179¹, a transverse section of the stem of a species of garlic (*Allium vineale*), the bundles are partially embedded in the outer part of the bast ring, and in 179³, a transverse section of the stem of a species of Solomon's Seal (*Polygonatum verticillatum*), the bundles are wholly embedded in the ring of bast. The first case is by far the most common, and may be regarded as characteristic of most dicotyledonous herbs and undershrubs; the second case obtains in many bulbous plants; whilst the third, the rarest of all, is only found in a few monocotyledons. The accessory parts occur either as band-like

projections from the bast tube, *e.g.* in the grass *Molinia cœrulea* (fig. 179 [4]), or as independent collenchymatous strands in the corners of the angular stem, as in the Woodruff (*Asperula odorata*, fig. 179 [5]), or, again, a circle of independent bundles of hard bast appears outside the bast tube, as in the stately umbellifer *Euryangium Sumbul* (fig. 179 [6]). In this plant the strengthening accessories are combined into independent simple girders and a canal filled with air is situated on the inner side of each of the flanges (*cf.* fig. 179 [6]).

The third group consists of all stems in which the flanges are developed as

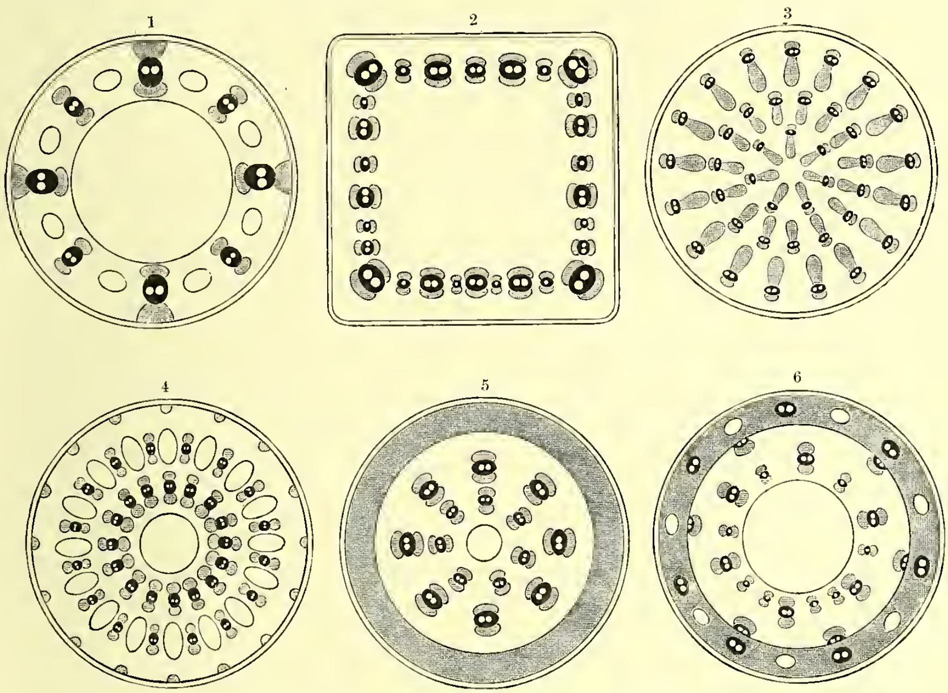

Fig. 180.—Transverse sections of erect foliage-stems with flanges developed as secondary girders.

[1] Tufted Scirpus (*Scirpus cæspitosus*). [2] Perfoliate Silphium (*Silphium perfoliatum*). [3] Black-stemmed Bamboo (*Bambusa nigra*). [4] Hard Rush (*Juncus glaucus*). [5] Common Reed (*Phragmites communis*). [6] Sugar-cane (*Saccharum officinarum*). In these diagrammatic figures the mechanical tissue is represented grey, and the vascular bundles black with white spots.

secondary girders. The web in these secondary girders always consists of vascular bundles, and the flanges themselves of hard bast. Sometimes the secondary girders are arranged in a single circle, but in most instances they form several concentric rings. In fig. 180 some of the most striking forms of this group are given diagrammatically. Fig. 180 [1] represents a transverse section of a stem of *Scirpus cæspitosus*, in which the secondary girders—arranged in a single circle—alternate with large air-spaces; fig. 180 [2] shows a similar section of the stem of the composite illustrated on p. 239 (*Silphium perfoliatum*), with its numerous series of secondary girders parallel to the four sides; and fig. 180 [3] is the transverse section of a bamboo (*Bambusa nigra*) in which the secondary girders are grouped in several concentric rings. Here, as in the first and second groups, accessory structures are present,

usually in the shape of tubes of hard bast, or as collenchymatous strands at the circumference of the stem. In the common Reed (*Phragmites communis*) this tube is quite uninterrupted and intact (fig. 180 [5]); whilst in the Sugar-cane (*Saccharum officinarum*, fig. 180 [6]) air-canals and vascular bundles are embedded in it. Much less frequently the strengthening is produced by bundles of bast which lie close under the epidermis of the stem and are not fused into a tube, as, for example, in the Hard Rush (*Juncus glaucus*), the transverse section of whose stem is shown in fig. 180 [4]. This rush is also characterized by the insertion of large air-spaces between the accessory strands which form the outer circle. Some of the erect stems here cited which resist bending are hollow within, whilst others are filled with a loose pith. In the diagrammatic figures the central cavity has been marked off by a circular line.

We should naturally expect to find that stems which are not able to rise from the ground without external support (including those numerous forms which are comprehended under lianes), would exhibit a structure different from that of erect stems. In climbing plants the young shoots alone require to resist bending; stems which have found a support can dispense with this property, and consequently with contrivances designed for this purpose. On the other hand, these plants, especially when perennial and lignified, must be protected against strains which are unavoidable in consequence of alterations occurring in their supports. Rocky walls and old battlements overgrown with climbing plants, of course, do not alter sufficiently to materially affect the stems attached to them; but it is otherwise where the climber is supported by a thickening stem. This class of support continues to grow, its stem increases in volume, the extent of the boughs and branches differs from year to year, and displacements and alterations in position occur which cannot but influence the plants climbing over them. Suppose a twining plant has embraced and twined around the stem of a young tree or the branch of a young shrub; years pass by and the stem of the tree has meanwhile increased a hundredfold in diameter, and the entwined branch of the shrub has been shifted about a metre; this cannot be without effect on the twining stem, and it requires no further explanation to see that it will exert a pull and lateral pressure. Perennial twining plants must therefore be so organized that their stem will bear tension and lateral pressure without injury, in other words, that their skin must be constructed to resist tension and compression. Resistance to strain is obtained in twining and interweaving stems in very different ways; in many cases, such as in the Rotang or Climbing Palm, by ample depositions of hard bast in the vascular bundles lying next to the axis of the stem; in other cases, *e.g.* in *Tamus* and *Dioscorea*, by a considerable thickening of the cells of the pith, and in others, again, *e.g.* in many species of Pepper, by the development of a ring of mechanical cells within the peripheral circle of vascular bundles. It is, of course, an advantage to the twining stem which requires protection against strain if the tissues lying next its centre possess a corresponding firmness. Thus we find unmistakable differences between these and erect stems; correlated with this is the fact that the pith, or the medullary cavity, in twining stems

is very much reduced, and that hollow twining stems, *e.g.* that of *Thunbergia laurifolia* (*cf.* fig. 128 [1], p. 477) are very rare. Perennial twining stems are usually protected from lateral pressure by a layer of collenchyma surrounding the conducting tissues like a mantle. Sometimes the collenchyma is also connected with bundles of bast, and there is no doubt that the same mechanical cells which strengthen the young twining stem protect it later on against lateral pressure.

Perennial climbers which have clambered up growing woody plants are exposed to the same dangers as described in the case of twining and interweaving plants, but in them tendrils as a rule afford a protection against tearing, and tissues providing a resistance to strain are absent from the stems themselves. In such plants it is the tendrils especially which are constructed to resist tension, as, for example, in the Atragene (*Atragene alpina*, the stem of which is shown in cross section in fig. 181). Tendrils, therefore, are evidently of complex structure. First, they must have a great capacity of resisting strain, but since they also have other functions to perform, and since these functions are different before and after the attachment to the support, very remarkable alterations in their inner structure must occur during development. At first they are required to resist flexion, for which purpose mechanical tissue is developed round the periphery; later on they have to resist tension which renders it necessary that mechanical tissue should be developed nearer the axis. An abundant development of mechanical tissue is also required on the convex side of the tendril bending round the support so as to increase the resistance to strain at that part, as also to prevent its unrolling from the support; such a development is actually to be seen in all tendrils.

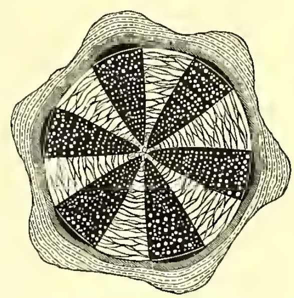

Fig. 181.—Transverse section of the climbing stem of the Atragene (*Atragene alpina*). The tissues are represented in the following way:—Soft bast, entirely black; wood, larger and smaller white dots on a black ground; the mechanical tissues, obliquely shaded; the cork (*periderm*), stratified; the loose reticular tissue, white with dark reticulations.

Older lignified stems of climbing and twining plants often exhibit a longitudinal splitting in the wood. Before they obtain their split appearance the narrow vascular bundles, which consist for the main part of wood, are isolated by a loose, wide-meshed tissue, and there is no central pith. In transverse section the narrow vascular bundles of such a stem resemble the spokes of a wheel, the weakly-developed mechanical tissue, which had served to protect against bending in the one-year-old stem, together with the cork (periderm), forming to some extent the rim of the wheel (*cf.* fig. 181).

When lateral pressure is brought to bear on these old stems, the cork and hard bast become ruptured at the places acted on, but only above the dead, large-meshed tissue; above the narrow vascular bundles they remain uninjured. The loose, dead tissue also ruptures and crumbles, and falls out of the grooves between the vascular bundles. These bundles, which now resemble plates or lamellæ of wood, lie above one another like the leaves of a book on the side where the pressure is felt. The wood looks as if it had been divided or split longi-

tudinally in this way. These proceedings have no disturbing influence on the functions of the vascular bundles, on the conducting power of the wood, or on that of the soft bast, though by the compression of the woody plates the shape of the cross section of the stem is altered. The lateral pressure exerted on the broad side of the plate-shaped vascular bundle is now harmless, and interrupts the transport of the sap neither in the wood nor in the soft bast.

Fig. 182.—Undulations of old ribbon-shaped liane stems (*Bauhinia anguina*) from an Indian jungle.

It has already been shown on p. 477 in one example (*Rhynchosia phaseoloides*) that injuries due to lateral pressure in the conducting tissues, especially in the soft bast, are also prevented in twining or climbing plants by the development of ribbon-shaped stems, and it need only be added here that with this flattening and ribbon-like shaping of the wood, and with the development of these wings, there is combined an economy of building materials. If the stem were cylindrical, an abundant mechanical tissue would have to be developed for the protection of the

soft bast against lateral pressure. The ribbon-shaped stem, however, can do very well without this, for the pressure along its edge is scarcely worth considering, and the soft bast is excellently protected against pressure on the broad side by the wood, which is broken up into a number of detached masses with the soft bast between.

There is no doubt that the spiral torsion of ribbon-like lianes (which is plainly shown in the illustration of *Rhynchosia phaseoloides*, fig. 127, on p. 475) increases the resistance to strain, a matter of some importance in all cases where growing trees or shrubs serve as supports, and where straining of the lianes clinging to them is unavoidable.

The undulations of ribbon-shaped liane stems in tropical forests may also be regarded as a protection for the sap-conducting tissues against strain. They occur in many bauhinias and in the peculiar species of *Caulotretus* known as monkey-ladders. The central part of the ribbon-shaped stem is alone strongly undulated, as may be seen in the portions of a *Bauhinia* represented in fig. 182; the two edges are much less curved and are often quite straight, forming a framework for the sinuous middle part. In the case of a longitudinal tension, at first only the frame is affected, the tissues in the centre can still uninterruptedly conduct the sap to and from the branches which arise from its broad surface.

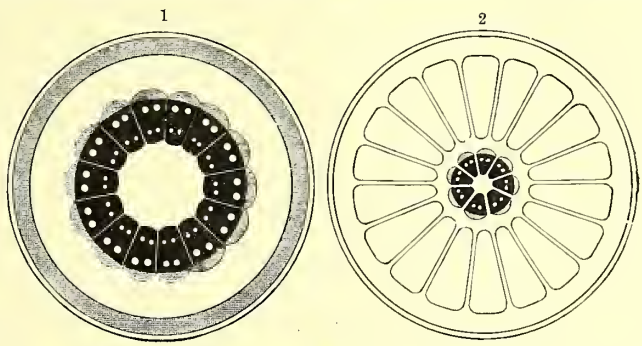

Fig. 183.

[1] Transverse section of a runner of the Garden Strawberry (*Fragaria grandiflora*) which lies on the ground. [2] Transverse section of the stem of the Water Milfoil (*Myriophyllum spicatum*). In these diagrammatic figures the mechanical tissue is represented grey, and the vascular bundles black with white spots.

Stems of water-plants as well as those embedded in the ground, and the stem-structures which lie on the surface of the ground, have, like climbing plants, little need for resisting flexion, but, on the other hand, require a greater resistance to pressure and strain. The soil or the surrounding water forms the immediate support for all these stems, and the arrangement of tissues suited to erect aërial stems would be useless here.

As a matter of fact they do not possess the peripheral strands of hard bast and collenchyma so characteristic of erect stem-structures; the vascular bundles are placed together near the centre of the stem, as is most advantageous for organs which have to resist strain, and the bast strands belonging to these bundles are relatively far removed from the circumference of the stem. The central pith is much reduced and is often completely absent (*cf.* the diagrammatic sections of a runner of the Garden Strawberry, *Fragaria grandiflora*, and of a hydrophyte, *Myriophyllum spicatum*, in the above figure).

The stems here considered are protected against the lateral pressure by a layer of thick-walled parenchyma (183 [1]), or by the strands of tissue crossing the larger air-canals which run longitudinally outside the circle of vascular bundles in the stem (183 [2]). In the underground stems of the Grass of Parnassus (*Parnassia palustris*), and of several other herbaceous plants, there is no pith, they exhibit a central strand of compressed vascular bundles and their structure is very similar to that of roots growing in the ground.

From this general account it is sufficiently evident that the arrangement of the tissues in stems does not so much depend upon whether the part in question belongs to a scaly stem, a foliage stem, or a floral stem, but rather upon its relations with the outer world, and in particular upon the influences exercised by the surroundings serving as a support or substratum. The stem, as the bearer of the foliage and flowers, must be so constructed that the organs named may be raised into the air, sunned, exposed to the wind and to the visits of flying insects and birds, and retained in the most advantageous posture in spite of all opposing influences of the environment. In such a stem are comprehended the various organs of food-conduction, the conducting capacity of which must not be impaired by pressure, flexion, or strain. All the functions of the stem are influenced and governed in a variety of ways by the varying circumstances of the habitat, and by the forms of foliage and flowers peculiar to each species. These functions are wonderfully correlated, and the different arrangement of the tissues in the stem in each individual case is nothing but the expression of the relation of the form to the conditions under which the plant lives.

THE FLORAL STEM.

The portion of the stem from which floral leaves proceed is called the floral stem (*thalamus*). It has the form of an axis, from the upper part of which project the carpels and stamens, and below these the perianth leaves. The floral stem, like every other, is built up of internodes whose number corresponds to the number of leaves on its circumference, standing vertically above one another; but since the vertical intervals are usually very small, the articulation of the stem is but seldom plainly visible to the naked eye. Below the perianth leaves only the floral stem appears more or less extended, and this portion is distinguished as the "flower-stalk" from the part which bears the perianth leaves, which is termed the "floral receptacle".

The flower-stalk (*pedunculus*) originates only in a few Rafflesiaceæ immediately from the tissue which represents the scaly stem. It is also of comparatively rare occurrence (restricted to a few annuals) that the stem proceeding from the bud of the hypocotyl (*i.e.* the main axis of the whole plant) passes directly into the flower-stalk and terminates in a floral receptacle. The flower-stalk often springs as a lateral shoot from the main axis of the plant, and generally it proceeds as a lateral axis from a stem structure which is itself only a lateral axis of the main

stem. The flower-stalk may originate from all three regions of the stem. In many parasites and saprophytes without chlorophyll it arises from the axil of a scale-leaf; in many annual plants, *e.g.* the Pimpernel and the Ivy-leaved Speedwell (*Anagallis arvensis* and *Veronica hederifolia*), it springs from the axil of a green foliage-leaf; more frequently, however, it is developed in the axil of a so-called *bract*, which is to be regarded as a floral-leaf.

The flowers are seldom isolated; in most instances they are associated in clusters, each cluster being termed an *inflorescence* (*inflorescentia*). For descriptive purposes it was found necessary to apply short names to the different inflorescences, and a special terminology was created by the older botanists which was most excellent, but which in modern times has become very cumbrous owing to the introduction and substitution of a host of Greek names which sound very learned, but are quite superfluous. It does not lie within the scope of this book to follow this terminology in detail. It is enough to bring forward the most prominent forms of inflorescence. I shall also touch as shortly as possible on the significance of these various associations and groups of flowers to the life of the plant, since this subject will be fully discussed in the second volume when describing the processes of fertilization, and especially the crossing of neighbouring flowers.

In describing inflorescences we shall frequently make use of the words "main axis" and "lateral axis", and in order to prevent misapprehension, it is as well to point out here that the main axis of the inflorescence, *i.e.* that part of the stem from which the flower-stalks branch off, is only in rare cases the direct continuation of the stem which proceeds from the bud of the hypocotyl (*i.e.* the real main axis of the whole plant). Even in the Hyacinth the green scape which rises from the ground, and branches off into a wealth of flower-stalks in its upper part, is not the original main axis, but a side axis springing from the axil of a bulb-scale. We are accustomed, however, to call that stem the main one which takes the lead in a certain region of the plant, forming buds which become lateral shoots in the axils of its leaves. The term "main axis" is therefore only relative; with respect to its lateral shoots it is a main axis, but with regard to the stem from which it originates, it itself must be looked upon as a lateral axis. In order to simplify the account and to shorten the descriptions of inflorescences, it is better to call the main axis—round which the individual flower-stalks are grouped as round a common centre, or which has conspicuously taken the lead in the whole system of axes—the "rachis".

Inflorescences have been classified into two groups, the centrifugal and centripetal. In *centrifugal* inflorescences the rachis terminates with a flower, but is retarded in growth and is outstripped by two, more rarely by three, lateral axes springing from the rachis below the first-formed flower-bud just mentioned. Secondary lateral axes may again spring from each of these lateral shoots, and their relative main axes may be again overtopped in the manner described. The flower-bud by which the rachis is terminated always opens first; then the flower-buds on the first series of lateral axes, then those on the second series of lateral

axes, and so on throughout the entire series. The unfolding of the flower-buds therefore proceeds always from the centre towards the circumference of the inflorescence in accordance with the succession of age, and consequently such an inflorescence may be termed *centrifugal*. The simplest form, the type of all centrifugal inflorescences, is the *simple cyme* (*cyma*). This presents only three flower-stalks, a central older one (the rachis) and two younger lateral ones. Since the latter spring at the same level from the rachis, the simple cyme has the appearance of a three-pronged fork. It often happens that the flower-bud on the rachis becomes stunted or does not develop at all, and then the inflorescence looks like a two-pronged fork (*e.g.* in many species of *Lonicera*). If the lateral axes arising from the rachis serve as starting-points for secondary lateral axes, and if the arrangement just described is repeated in them, a *compound cyme* (*cyma composita*) results. The flower-stalks may be arranged either as two prongs or three prongs in the compound cyme, and this branching may be repeated almost indefinitely, as is the case, for example, in *Gypsophila paniculata*. When one of the opposite flower-stalks, or lateral axes of a cyme, does not develop, while the other, on the contrary, becomes very vigorous and projects beyond the rachis, this lateral looks like the main axis, and at first sight the rachis is mistaken for a lateral shoot. Similarly on this vigorous lateral axis, one of the secondary lateral shoots does not develop, while the other continues to grow the more strongly. If this happens continuously, the form of cymose inflorescence called *scorpioid* (*cincinnus*) is formed, numerous modifications of which have been distinguished. If the flower-stalks of a compound cyme are all plainly visible and the whole inflorescence bulky and diffuse, it is termed a *panicle* (*panicula*); if the flower-stalks are much shortened and the flowers consequently crowded thickly together, the inflorescence is called a *fascicle* (*fasciculus*). Caryophyllaceæ, Labiateæ, and Boragineæ exhibit an almost inexhaustible variety of cymose inflorescences.

Centripetal inflorescences may be recognized by the fact that the rachis terminates in a bud which is the youngest structure of the whole inflorescence, the flower-stalks which spring from the base of the rachis being the oldest lateral axes. Looking down from above on such an inflorescence, or observing the points of insertion of the individual flower-stalks in horizontal projection, the lowest, and at the same time the oldest flower-stalks, are seen to stand at the periphery, the youngest at the centre of the inflorescence. The flowers on the oldest flower-stalks unfold first, those of the youngest last; the blossoming therefore proceeds in a centripetal direction. The rachis is terminated as a rule by a stunted bud which does not complete its development; occasionally, however, this bud does develop; it assumes the form of a foliage-bud from which later on is formed a leafy shoot, as can be seen especially in several Australian Myrtales from the section of the Leptospermeæ (*Callistemon, Metrosideros, Melaleuca*), and also in many Bromeliaceæ (*e.g.* the Pine-apple, *Ananassa sativa*). Among centripetal inflorescences may be distinguished the *raceme* (*racemus*) with elongated

rachis and evident flower-stalks; the *spike* (*spica*) with elongated rachis and extremely reduced flower-stalks; the *umbel* (*umbella*) with an extremely reduced rachis and elongated flower-stalks; and the *capitulum* (*capitulum*) with a very short thick rachis and exceedingly reduced flower-stalks. All these inflorescences are connected together by intermediate forms, of which the *corymb* (*corymbus*)—especially characteristic of Cruciferæ—forming a link between the umbel and the raceme, deserves special mention. The capitulum exhibits the greatest variety, but this is produced less by the different forms of the floral stem than by the shape of the floral leaves, especially of the numerous crowded bracts which collectively surround the flowers as a cup-like envelope. A form of spike with thickened rachis, called a *spadix* (*spadix*), is also worthy of note, and also the spike known by the name of *catkin* (*amentum*), the flowers of which are devoid of perianth-leaves, and spring from the axils of scale-like bracts. The whole catkin falls off after flowering, or after the ripening of the fruit, a separation of the tissue and a detachment of the cells having previously occurred at the base of the rachis.

When spikes are themselves arranged in a spicate manner, the whole inflorescence is called a *compound spike* (*spica composita*); racemes grouped into larger racemes form a *compound raceme* (*racemus compositus*); and umbels when arranged in larger umbels form a *compound umbel* (*umbella composita*). The first two occur very often in grasses, the last in umbelliferous plants. The term panicle is also often applied—rather loosely—to any compound raceme.

Various combinations of the above simple inflorescences have been distinguished, particularly combinations of centripetal with centrifugal inflorescences. Capitula and compound umbels which are arranged in cymes, and cymes which succeed one another in a spicate or racemose manner are of very common occurrence. In these inflorescences the order of blossoming becomes altered. Of the many umbels which are grouped together in an extensive cyme, the central umbel is the first of the series, but it is the flowers on its periphery and not the central flowers which open first. If cymes are arranged like a spike, the lowest, *i.e.* those on the periphery of the whole inflorescence blossom first, though in each individual cyme the central flowers are always the first to open.

The order of blossoming, which is determinate for the flowers of every given species, is related to the transmission of the flower-dust or pollen to the stigma, and therefore with the processes of fertilization. When in one and the same flower the organs in which the pollen and those in which the ovules are developed stand closely side by side, it might be thought that the pollen would be certain to reach the adjoining stigma. But this opinion is not confirmed by experience. It has been demonstrated, on the other hand, that it is of advantage to the plant that the pollen of one flower should reach the stigma of another, indeed of the flower of quite another plant often some distance away; thus we find that cross-fertilization is aimed at, at any rate at the commencement of the flowering period. I purposely say "aimed at", and avoid saying that crossing of different plants

always takes place, because very often the crossing is prevented from some cause or another. The event of failure is also actually provided for; in case the crossing of different plants does not succeed, care is taken that in the second stage of flowering the pollen should reach the stigmas of the neighbouring flowers of the same plant. In most plants only when this plan also fails, and at the last moment, so to speak, does the pollen developed in the stamens of a flower reach the stigma of the same flower which hitherto has remained intact although placed in the closest proximity. The wonderful and extremely complicated contrivances which are met with for the attainment of this threefold aim will be considered fully in the second volume; but they must here be mentioned cursorily, because the peculiar grouping and the remarkable order of the opening of the flowers represent contrivances which render possible the crossing of neighbouring flowers, and because the shape of the inflorescence can only be comprehended in connection with these contrivances.

In thousands of different species it can be seen that in the event of failure of crossing between flowers of different plants, a cross-fertilization between neighbouring flowers is brought about by elongations, shortenings, depressions, and various other alterations of position, sometimes of the style, sometimes of the stamens, of the floral receptacle, or of the flower-stalks. In the racemose inflorescences of *Eremurus* (a liliaceous plant) the long styles of the lower flowers, which are directed towards the rachis, bend upwards, towards the end of the flowering period, in order to obtain pollen from the younger flowers above; and the same thing occurs in the floral fascicles of a Woodruff (*Asperula taurina*), in which the styles bend down laterally to the neighbouring flowers in order to come into contact with their pollen-laden anthers. The stamens of the Wayfaring Tree (*Viburnum lantana*) curve down towards the neighbouring flowers so that the pollen, falling from their anthers, must alight on the stigmas of these neighbouring flowers. The same thing happens in *Hacquetia, Chærophyllum hirsutum, Siler trilobum*, and various other umbelliferous plants. In these we find that the stamens of the flowers in the centre of the umbel stretch out so far that their pollen-laden anthers are situated above the stigmas of the neighbouring older flowers, already deprived of stamens, at the periphery of the umbel. In *Anthriscus sylvestris* the younger umbels are placed above the older so that the pollen falling from the former must necessarily reach the latter standing below them.

In numerous composites, especially in asters and Golden-rod (*Aster* and *Solidago*), as well as in species of *Cacalia, Senecio*, and *Arnica*, the tubular florets are so arranged in the centre of the capitulum that the pollen expelled from the younger, inner flowers necessarily falls on the stigmas of the adjacent, outer flowers without the aid of any special elongation or curvature. In those composites, on the other hand, of which the Chamomile (*Matricaria chamomilla*) may be taken as a type, the stigmas of the older, peripheral flowers are brought under the pollen falling from the inner, younger flowers by an elongation of the arched or conical rachis, and by the slight raising or displacement of the flowers of the capitulum so pro-

duced. Very many composites with ligulate florets, *e.g.* the species of Salsify and Hawkweed (*Tragopogon* and *Hieracium*), periodically open and close their capitula, *i.e.* the ligulate portions of their flowers curve for a time outwards, so that the upper side is turned towards the sky; they then again become erect, curve inwards, and at length close tightly together. In this closing of the capitulum the stigmas of the peripheral flowers become pressed against the pollen of the central ones, and in this way a crossing is necessarily brought about between neighbouring florets. All these crossings, however, could not occur if the flowers of a plant were developed at great distances from each other and all unfolded at the same time, and there is no doubt that the formation of capitula, umbels, close racemes, spikes, and cymes, ranks as an important contrivance for accomplishing the cross-fertilization of the flowers.

Another advantage obtained by the close grouping of the flowers consists in the fact that certain portions of one flower serve as temporary resting-places for the pollen falling from an adjoining flower, which at the moment of dehiscence is not yet ready for dispersion in the air. In order to clearly explain this contrivance, which may be observed in catkins, I will take the case of the flowers of the Walnut (*Juglans regia*) figured on the next page. As long as the male inflorescence is immature, the flowers are crowded together in a short, thick spike, the free end of the rachis being directed upwards. Simultaneously with the development of the pollen in the anthers, however, very remarkable changes are brought about in a short time in the whole inflorescence. Within a few days the rachis elongates to three or four times its former length, and becomes limp and pendent; the flowers are in this way somewhat separated and brought into an inverted position, so that now the open side of each flower is directed downwards, and the lower side upwards. When the wind is still, the anthers, hanging on thin short filaments, open, and the pollen rolls out of them as a powdery mass. It does not fall directly into the air, but, first of all, drops on to the under side of a neighbouring flower which previously, in the erect spike, stood above the anthers in question, but now that the spikes have become pendent, is situated below them. This under side is plainly excavated as a depression, and the pollen of the flower above is deposited in it for a time, as shown in the illustration over page (fig. 184 [2]). The pollen has to reach the stigmas of flowers developed a long distance from the catkins, often on other branches up above. It would be highly disadvantageous, if, after the dehiscence of the anthers, the pollen should fall immediately to the ground; it would then be lost and wasted, and neither favourable winds nor lightly hovering insects would be able to carry it from the earth to the stigmatic flowers on the branches of the tree. But in the depressions on the under sides of the flowers, as if in a waiting-room, it occupies the most favourable position conceivable. While there is no wind, the tassel-like spikes are undisturbed, and the pollen remains quietly in its temporary resting-places; but as soon as a gust of wind comes, the spikes oscillate, swinging to and fro like pendulums, and the pollen, emptied and blown out of the pit-like cavities, is carried to the neighbouring branches and whirled round the tree-crown on to the stigmas, in

the form of small clouds of dust. In this instance the pollen is not only prevented from being wasted by the spikate arrangement of the flowers, but this further advantage is obtained, that each flower shelters the pollen of the neighbouring flower in a safe harbour until it can be transmitted by a favourable wind to its desired goal.

Fig. 184.

[1] Branch of the Walnut-tree (*Juglans regia*) with hanging male catkins, and a small cluster of female flowers; natural size
[2] The tip of a male catkin; enlarged.

The grouping together of the flowers also offers numerous advantages with regard to flower-visiting insects. Flies, bees, and humble-bees do not content themselves when seeking honey with taking it from single flowers, but climb from one flower to another, from below up to the highest points of the spikes and racemes,

or walk from one fascicle and umbel to a neighbouring one as if over a flower-strewn surface, thus moving the pollen from place to place and effecting innumerable crossings which would not take place so easily if the flowers were isolated and not collected into inflorescences with a definite order of blossoming. The likelihood of a crossing between different flowers is of course increased with their greater number, and consequently plants with grouped inflorescences have so far an advantage over those whose flowers unfold singly at greater distances. Isolated flowers, it is true, possess large, brilliantly-coloured perianth-leaves which serve to allure honey-seeking animals on the wing; but, on the other hand, the same effect is produced by the accumulation of many small flowers, and an attraction is also afforded by the development of so-called ray florets on capitula and umbels, as well as by the brightly-coloured bracts forming a tuft on the top of cymose and spiked inflorescences, which is no less effective than the largest corolla. This explains why 90 per cent of plants visited by winged insects bear inflorescences and not isolated flowers. Large isolated flowers only serve the purpose of larger honey-seeking animals, of such butterflies and moths, humming and other honey-seeking birds, which would not be able to obtain the honey from small, conglomerated flowers. But it is a well-ascertained fact that the number of small flies, bees, wasps, and humble-bees which visit flowers greatly exceeds that of larger animals, and this explains why clusters of small flowers occur much more frequently than large single flowers.

Remarkable correlations with the animal world also exist in other regions of the plant, but in no other part of the stem do they appear so striking and so manifold as in the floral region. Nowhere else can the harmonious co-operation of the members, the practical division of labour, and the mutual aid for the attainment of an end, be seen so plainly and convincingly as in the inflorescence. In many capitula and umbels one portion of the flowers forms the pollen; another develops the ovules; a third allures insects; and a fourth prevents the depredations of unwelcome visitors. Most remarkable of all, this practical division of labour within a single inflorescence does not terminate even with the fading of the flowers, but is still continued in the same parts during its subsequent passage into a fruiting state. Many processes give us the impression that the flowers collected in a raceme, umbel, or cyme mutually understand one another; thus, for example, in the Cruciferæ it often happens that older flowers, whose stigmas have already withered, and which have also entirely lost their pollen, allure insects to the adjoining younger flowers, since now, instead of falling, the petals enlarge and adorn themselves with conspicuous colours, visible at a distance. It also frequently happens that older flowers, whose time is over, vacate the most advantageous position for blossoming in favour of neighbouring younger flowers. When the flower of a nasturtium (*Tropæolum*) fades, its flower-stalk bends downwards, contracts in a spiral, and hides under the green peltate foliage-leaves, while a new bud pushes into the place where the older flower formerly stood; this bud opens next day and awaits insect visits, and hasty observers might think that the same flower had remained there for more than a week. The same thing occurs in *Linaria cymbalaria*, *Ledum*

palustre, and numerous species of clover. In the Alsike Clover (*Trifolium hybridum*) growing abundantly in marshy meadows, the older flowers not only sink down in order to give the place best adapted to insect visits to the younger ones, but their corollas turn a beautiful red colour, contrasting vividly with the white of the younger flowers. The contrast is visible at a great distance and serves to attract insects. In the curled inflorescences of the Comfrey, Forget-me-not, and Viper's Bugloss (*Symphytum, Myosotis, Echium*), and many other Boragineæ, the inflorescence may be seen to unfold and fix itself, so that the flowers in turn are placed in the position in which they are best seen by and most accessible to flying insects; meanwhile the older flowers, whose time is over, and to which insect-visits are of no further use, move out of the way of those which have just opened, and always choose their position so as not to obstruct the entrance to the new flowers of the same inflorescence. In this process not only the flower-stalk but the rachis of the whole inflorescence takes part, and it is interesting to observe how even widely distant parts of the stem are sympathetically affected, so to speak, and how all the different parts of the system of axes are extended, raised, depressed, and curved exactly as required for the purpose of affording the most favourable position to each flower in turn.

The most remarkable thing of all, however, is that under certain conditions, which only occur exceptionally, the most favourable position for the flowers is striven after and obtained by means of curvatures produced in the stem in places where, in the ordinary course of things, such changes would not have occurred. When the Wood Forget-me-not, Larkspur, Monkshood, Adenostyles, the Willow Herb (*Myostis silvatica, Delphinium elatum, Aconitum variegatum, Adenostyles alpina, Epilobium angustifolium*), and numerous other undershrubs whose stiff, erect stems are terminated by a group of brilliantly-coloured flowers adapted to insect-visits, are pressed down and extended on the ground shortly before the unfolding of the flowers by some unusual occurrence, so that the normally erect inflorescence lies on the soil, the stem will be seen to form a bend below the inflorescence, as it is no longer capable of raising up the whole length, and the portion bearing the flowers will be elevated until it again becomes erect, and its flowers are again placed in a position favourable to insect-visits. This curvature is no ordinary phenomenon of growth, for the portion of the stem forming the bend has already ceased growing, and the curvature does not extend to the rachis of the inflorescence, but takes place below it, being strictly localized there; the rachis itself, which is raised up, always remaining straight. Finally, no kind of stimulus can be shown to affect the internodes in which the bend is formed. Contact with the soil and illumination from above act just in the same way on it as on the internodes above and below it. No external causes whatever can be assigned to this knee-shaped bending, and only this much is certain—the bending could not take place at a spot better suited to the purpose of restoring the flowers once more to a favourable position.

The flowers of more than an eighth part of all flowering plants are grouped

together into capitula, this inflorescence being the commonest of all. Next to it comes the cyme with its numerous modifications, and then the umbel, the raceme, and the spike. Of all plants, perennial undershrubs exhibit the most extensive inflorescences, in comparison with the size of the whole plant. Many of them only send up an axis every year which bears a few large foliage-leaves at the base, is beset with scale-like bracts further up, and terminates in numerous umbels, racemes, or cymes, forming a single gigantic inflorescence. As an example of this form found in the East, especially in the steppes of Persia and Turkestan, may be instanced *Euryangium Sumbul.* This umbelliferous plant, abundant near Pentschakend, south of Samarkand in Southern Turkestan, develops at the beginning of the vegetative period some five radical foliage-leaves divided into innumerable lobes, and having a musky odour; these leaves only retain their fresh green for a few weeks and then wither and become bleached, turning a pale violet colour comparatively early. As soon as these radical leaves have begun to change colour a leafless, blue-tinted, asparagus-like, slim shoot, 4–5 cm. thick, rises above the ground and branches repeatedly in its upper third into numerous umbels. A whole series of oriental Umbelliferæ behave like this strange Sumbul plant, especially those of the genus *Ferula,* as also the *Scorodosma Asa fœtida,* yielding the notorious asafœtida, and several Cruciferæ. One of these cruciferous bushes, *Crambe cordifolia,* develops within a few weeks an inflorescence with long branches, projecting like spars, about 2 metres high and almost as much across. The *Agave Americana,* known as the Century Plant (illustrated on p. 657), is also similar to these plants. The stem, 5–7 metres high and 6–12 cm. thick, which rises above the rosette of thick fleshy foliage - leaves with spinous margins, is covered only with dry, scale-like leaves, without chlorophyll, and forms the rachis of an inflorescence which is one of the largest in the whole vegetable kingdom.

In contrast to the undershrubs, whose rapidly-growing stems, terminated by large inflorescences, remain herbaceous and wither and die down to the ground without lignifying after the maturing of the fruit and seeds, woody plants, especially trees, produce as a rule only small inflorescences. It is true that their number is correspondingly large. The perianth-leaves are frequently green, and the inconspicuous inflorescences distributed between the foliage-leaves are then entirely invisible at a little distance. Often, however, numerous small but brightly-coloured inflorescences are crowded so close together as to be inseparable; in cases where the flowers unfold before the green foliage, as, for example, in Almond and Cherry trees, each tree from a distance resembles a gigantic bouquet of flowers.

Only a few inflorescences are found in palms, but they are usually very large and many-flowered. Generally speaking palm inflorescences are the largest of all. Those of the Doum Palm (*Hyphæne thebaica*) and of several species of *Phœnix* are more than a metre, those of *Raffia Ruffii* and of *Plectocomia elongata* 2 metres long, and the Talipot Palm (*Corypha umbraculifera*), illustrated on p. 289, is celebrated as possessing the largest inflorescence of all plants. This remarkable diœcious palm grows comparatively slowly: its caudex often takes 30–40 years

before attaining a height of 20 metres, and during this period flowers never appear. Not until the caudex has attained its full size of 22 metres does the inflorescence spring from its apex, the rachis reaching an additional height of 14 metres. Twelve or thirteen rounded branches are given off from this rachis, the longest of which becomes 6 metres long. All the branches terminate in numerous branchlets and twigs, and are richly covered with flowers. The whole inflorescence when fully grown exhibits the fabulous height of 14 metres, with a breadth of 12 metres. As soon as the flowers open, the fan-like foliage-leaves below begin to fade and often all fall off during the flowering period, so that the shaft alone remains, bearing the inflorescence at its apex. The flowering period lasts for 3–4 weeks. As soon as it is over and the fruits matured, the whole plant dies down, as in *Agave Americana.* Each of these palms therefore only blossoms once in its life.

With this, the largest inflorescence, may be contrasted that which is regarded as the smallest of all, viz. the capitulum of *Nananthea,* only 2–3 millimetres in diameter, found growing on the mountains of Corsica.

The size of the inflorescence, and that of the flowers composing it, do not vary proportionately. Extensive inflorescences usually have very small flowers, and *vice versa,* but a universal rule cannot be laid down in this matter. The inflorescence of *Paulownia imperialis* has 100 large flowers, and that of *Spiræa Aruncus,* equal in extent, 10,000 small ones. The Talipot Palm is said to bear about 100,000 flowers in its gigantic bouquet. In simple cymes it often happens that the central flower is not developed, and the whole then consists of a pair of flowers, usually curiously united, as can be seen in many species of the genus Honeysuckle (*Lonicera Xylosteum, nigra, cœrulea, alpigena*). In many Acanthaceæ, bindweeds, and labiate flowers, on the other hand, it is observed that the two lateral flowers of the three of a simple cyme are suppressed, and that only the central one attains development, in which case the whole inflorescence is represented by a single flower.

The *floral receptacle* (*podium,* also *torus*), *i.e.* that part of the floral stem from which the perianth leaves spring, is always somewhat thickened in comparison with the flower-stalk, and may be either conical or disc-shaped. The *conical* receptacle (*conopodium*) has the form of a cone, being sometimes elongated and peg-shaped, but often short and but slightly curved; it is always narrowed from its base, the thickest part, up to the apex. Unlike the very simply-constructed conical receptacle, the *disc-shaped* receptacle (*discopodium*) presents a great variety of form. The apex of the floral axis is retarded in growth, the tissue round it thickens and becomes flattened, or surrounds the apex with a circular cushion or rampart often rising so much above the apex that the whole receptacle has a crater-like or cup-shaped appearance. In the first case, viz. when a circular wall has been formed, it surrounds the pistil, developed in the centre above the apex, without overtopping it, as, for example, in the flowers of Orange and Lemon trees. The stamens and perianth-leaves usually arise outside, less frequently within the ring, and most rarely of all from the edge of the ring itself. When a cup-shaped

receptacle has been formed, the end of the axis is overtopped by the edge of the cup, and the actual apex of the receptacle must be sought at the bottom of the cup. The stamens and perianth-leaves then spring in most cases from the edges of the cup. In many instances the carpels also arise from the edges and cover over the crater-like depression of the receptacle. More frequently the carpels are developed at the bottom or on the inner walls of the cup, and then either a single carpel is to be seen in the depression, as, for example, in cherry flowers, or several carpels, as, for example, in the rose. Sometimes the pistil developed at the bottom of the cup-shaped receptacle is fused with the inner wall of the cup, as, for example, in the flowers of apple and pear trees.

The disc-shaped receptacle is not, as in the examples selected, always developed symmetrically all round. In flowers which project laterally from an erect rachis, the circular wall is often interrupted, or instead of the circular disc a one-sided projecting ridge or cushion is seen. The ring is often replaced by a circle of protuberances or papillæ, or the receptacle is drawn out on one side, taking the form of a peg, a tongue, or a scale.

Honey is usually secreted from that tissue of the disc-shaped receptacle which does not pass over into perianth-leaves, but which projects and is inserted between the whorls of perianth-leaves, stamens, and carpels in the form of knots, warts, cushions and rings; this serves to attract insects whose visits are of use to the flowers in effecting fertilization. The part of the receptacle which is developed as the under-structure or envelope of the carpels, on the other hand, very often becomes a part of the fruit. In most cases, however, the significance assigned to the various developments of the receptacle in respect to the life and welfare of plants is not yet rendered sufficiently evident. That the relations between receptacle and fruit-formation are of the greatest importance is the only thing that can be affirmed with certainty, but why in one instance this and in another that form of receptacle is produced remains entirely enigmatical. The opinion has been repeatedly stated that all the architectural conditions of plants are not necessarily beneficial, and that the forms in which the individual organs and plant members appear fall into two groups—those whose use to the species in question is obvious, and those in which this is not the case. The former were said to be variable, the latter invariable. This hypothesis was forthwith raised to a dogma, and it was further concluded that only structures whose significance in the life of plants cannot be explained are of use in the limitation and systematic determination of species and groups of species. I cannot justify this notion, and maintain rather that nothing is ever formed in a plant which is not beneficial, which is not even indispensable to it. Those organs which are so often termed "reduced" are not without importance in the life of plants; they are rather developed in this only apparently-reduced form for the welfare of the whole, and cannot be dispensed with without injury. If they were unnecessary, they would also be absent. The plant builds up nothing superfluous, and no hair, no cell even, is developed without some purpose. It is hazardous and unwarranted to say that

this or that structure is useless, and to be interpreted only as the remnant of an organ which was developed more fully a long time ago in some ancestral species to which it was indispensable. When we cannot immediately see the advantage of any structure, we are not justified in saying that in its particular form it is worthless or indifferent to the plant. The saying *dies diem docet* is perhaps nowhere more applicable than to questions concerning the significance of forms. How many structures which were enigmatical a century ago are now recognized as essential members of very various contrivances, and explained in all their details; their recognition being regarded as an incontestable scientific thesis! The tendency of our age, indeed, is not merely to regard and describe forms as mute puzzles of nature, but to comprehend their value as parts of a living entity. Therefore I doubt not that sooner or later the importance of the different forms of floral receptacles will find interpretation and explanation in the individual species to which they belong.

A peculiarity which distinguishes the floral receptacle from all other stem-structures, which has to be considered here in conclusion, is its limited growth. As long as the receptacle forms floral-leaves on its periphery it always continues to elongate to some extent, although the increase in length is inconsiderable; but after the production of the highest floral-leaf no further divisions take place in the cells of the apex, and the elongation of the axis is at an end, not temporarily, but permanently. This fact is of importance inasmuch as one of the few differences which have been established between stem and leaf undergoes a material restriction thereby. But the limited growth of the floral receptacle has also a special significance in regard to the architecture of the whole plant. The portion of the stem which forms the floral receptacle separates usually with the flower-stalk, and not infrequently even with the whole rachis of the inflorescence from the floral stem below, as soon as the leaf-structures proceeding from the receptacle have fulfilled their function; or, in other words, the flower and fruit-stalks become detached as soon as the perianth-leaves have withered, the stamens emptied, and the fruits matured—a process which reminds us of the detachment of those foliage-leaves which are no longer able to fulfil their allotted tasks. Just as a scar arises, or a withered stump remains behind where once a leaf existed, so a healing tissue is formed at the place where a portion of the floral stem has separated off, and at this spot no further stem growth takes place. If the shoot terminates with a single flower, or an entire inflorescence, it can no longer elongate in a straight line after the fruit has fallen; its apical growth is terminated for ever. Lateral shoots, on the contrary, may spring from the axils of lower foliage-leaves and may grow up beyond the scarred places, a fact which of course materially influences the type of branching and the architecture of the whole stem. This influence is very noticeable, especially in tall woody shrubs and trees. Where for instance the scarred apex of a branch is overtopped by two lateral branches springing close under the scar, a more or less regularly two-pronged fork results; and when the process is repeated on the prongs of this fork, a very

ornamental form of branching is produced which may even be recognized on the older boughs, and gives a characteristic habit to the shrub or tree. Although the annual growth in height in woody plants branching in this fashion is only slight, the crown grows in breadth to a striking degree, and the older, leafless boughs have usually the appearance of horns or of an interwoven lattice-work spreading out above, as may be seen in a remarkable manner in the Stag's-horn Sumach (*Rhus typhina*), and also in several species of Horse Chestnut (*e.g. Æsculus flava* and *discolor*). In the Oleander (*Nerium Oleander*), and frequently in the Mistletoe (*Viscum album, c.f.* fig. 46, p. 206), the scarred apex of the main shoot is overtopped by a whorl of three lateral shoots, which produces another characteristic modification of this form of branching.

The internal structure of the floral stem, especially the arrangement of the mechanical tissue, is always adapted to the tasks naturally assigned to the bearer of the flowers and fruits. When the floral portions and the fruits proceeding from them are to be maintained in an erect position, the stalks and also the rachis in question are constructed so as to resist flexion. The stalk and rachis of pendent flowers, and especially of heavy pendent fruits, are, on the other hand, constructed to resist tension; in both cases they are provided with mechanical tissue suitably strengthened and arranged. Frequently the same bast cylinder which afforded the resistance to flexion in the erect flower-stalk at the time of the opening of the flowers has subsequently to provide a resistance to strain, as when a pendent fruit is produced from an erect flower. The converse also happens, and not infrequently erect fruit-stalks, very resistant to bending, which take part in the dispersion of the seeds, are developed from pendent flower-stalks with the capacity of resisting strain. For the rest, in all these alterations of position, the turgescence of the parenchymatous tissue on the periphery of the flower-stalk plays a prominent part.

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4. FORMS OF ROOTS.

Relation of external and internal structure to function.—Definition of the root.—Remarkable properties of roots.

RELATION OF EXTERNAL AND INTERNAL STRUCTURE TO FUNCTION.

Every seed is provided by the parent plant with as much starch, fat, sugar, and other materials as are necessary for its further independent development. The germinating seed respires, provides itself with water, dissolves the materials stored up in its cells, augments the number of its cells, and increases in size. The food-substances of the soil at first take little or no part in these processes. But as the seed germinates its aim is to develop organs capable of laying the food-substances contained in the soil and air under contribution, and of manufacturing

fresh building-materials as those with which it was provided by the parent become exhausted. The tissues of the young seedling always contain cells for the absorption of the dissolved food-salts and gases; these enter immediately into a close union with the substratum, whether it consists of inorganic earth, of decaying organic matter, or of a living host-plant.

There are plants in whose seeds no differentiation into various parts, no separation into embryo and food-stores, can be recognized, and in the seeds of many thousand species we cannot even distinguish an embryo with cotyledons, in which case the whole of the group of cells forming the seed must be regarded as embryo. This group of cells first grows up, at the expense of its own materials, into a structure having the form of a small tubercle, which on one side joins with the substratum by absorbent cells, and on the other sends out a shoot, but develops no system of tissues which could be called a root. This occurs, for example, in *Monotropa* and in the Coral-root (*Corallorhiza*), described on p. 111, which are usually termed rootless plants. In other examples of this group, in which the undifferentiated embryo grows up directly into a small tubercle or stem, warts, papillæ, pegs and vermiform structures, equipped with absorbent cells, develop on this tubercle, and join with the substratum; these are, therefore, of the nature of roots. These structures always originate in great numbers from the tubercle, *i.e.* from the enlarged developing embryo; in many orchids living epiphytically on the bark of trees they are formed on the side turned towards the tree; in parasitic Orobanchaceæ around the thickened lower end of the tissue-body (*cf.* figs. 34^{11} and 34^{12} on p. 173), and in species of *Cuscuta* and *Cassytha* laterally on the thread-like embryo where it has attached itself to a host-plant.

In plants whose seed contains an embryo differentiated into stem and leaf, only a single, wart-like or conical body arises at one end of the hypocotyl, opposite the bud of the epicotyl; it grows at germination into a cylindrical root provided with absorbent cells, and later appears as a straight, downwardly-directed continuation of the hypocotyl.

Neither the abundant roots proceeding from the undifferentiated embryo, nor still less the single root springing from the membered embryo, suffice for the requirements of the shoot arising from it. In proportion as this increases in size, forming one internode above another, developing leaves with buds in their axils which grow out into lateral shoots, the need of water and food-salts becomes greater and greater. Fresh sources must be obtained for these materials, and new conducting mechanisms must be established—in a word, new roots must be formed. When only a single primary root is present in the embryo, the new roots frequently spring from this as lateral branches, and it is customary to say that the primary or main root has become branched, that it has formed lateral roots. Of course each branch can again ramify, and indeed the branching is often repeated beyond measure. The branched root (*radix ramosa*) is to be seen especially in annual land-plants with erect leafy stems. Almost as often it happens

that the root proceeding from the embryo perishes as soon as it has emerged from the seed, and that then many new roots originate from the hypocotyl, close to the place from which sprang the dead primary root; or that roots are developed on the lower end of the epicotyl embedded in the ground—in which case they stand closely crowded together in great numbers forming a cluster, and are then known botanically as fascicled roots (*radix fasciculata*). But many roots also arise further up on the shoot-axis, not only in the region of the scale-leaves, but also, if required, in the foliage portion of procumbent, erect, and climbing stems, and under certain conditions even on the foliage-leaves. These structures which may originate from the stem at all stages of age and height, and even from the leaves, are called adventitious roots (*radices adventiciæ*).

When roots are developed on a leafy stem, it is noticed that their places of origin are near the points of insertion of the leaves. In epiphytes, especially in aroids and orchids living on the bark of trees, they are sometimes seen to be so distributed that a single root, a pair of roots, or a whole fascicle of roots, arises at exactly defined places on the stem. Each internode in these plants has its own roots, and is therefore almost independent of neighbouring internodes, so that, supposing one or both the adjoining internodes should die from some cause or other, it can maintain itself independently (*cf.* fig. 51, p. 224). In stems which lie on the ground, as in runners, the roots always originate only at the nodes, *i.e.* at the commencement of an internode. In the underground stems known as rhizomes, the roots are distributed in the same way. When the older internodes of these runners and rhizomes die off behind, the next youngest are not injured, for they are already provided with roots of their own, by whose help their requirements of water and food-salts are supplied, and by which they are firmly fixed in the ground. The general symmetry and geometrical distribution of the places of origin, as shown in leaves, is, however, absent in the majority of roots, the arrangement being frequently quite irregular, especially in underground, much-branched roots where influences operate on them which will be spoken of later.

The functions assigned to the root are: first, the absorption and transport of water and of food-salts dissolved in water, and second, the fixing of the whole plant in the substratum. In most cases this twofold function is performed by the same root, but occasionally a division of labour occurs, so that one portion of the root-system serves only for the absorption of food, and another for the fixing in the substratum. For instance, the repeatedly mentioned *Tecoma radicans* has two kinds of roots; the first underground, absorbing water and food-salts from the soil, and the second the clinging roots (figured on p. 479), by which the light-avoiding shoots are attached to places from which no fluid nourishment could possibly be absorbed. When one of these shoots is cut across below the place at which it is fixed by roots to a wall or rock-face, the part above the section forthwith dries up, even although these roots and the substratum are kept continually moistened and damp.

Roots of biennial and perennial plants, in regions where the vegetative activity

is temporarily interrupted by drought or cold, frequently have a third function to perform, viz. that of storing up starch, fat, sugar, and other reserve food-materials. Obviously the parts concealed in the ground are protected in a high degree against aridity and frost in countries with long-continued summer drought or with severe winters, and therefore the underground root-structures principally, together with underground parts of stems and the scale-leaves arising from them, can be used most advantageously as reservoirs for the materials formed in the green organs above ground during the short period of vegetation.

The variety of functions assigned to roots, the diversity of the substrata, and the peculiar conditions of the habitat and climate render necessary a large number of different forms, the most noticeable of which bear special names in botanical terminology, and will be briefly enumerated here. According to the substratum into which the roots penetrate, and from which they derive water and food, we may distinguish between subterranean, aquatic, aërial, and parasitic roots.

Subterranean roots (*radices hypogaeæ*) push their ends, which are beset with root-hairs, into the ground with great energy, and are entirely covered over with soil, or at any rate in so far as their absorbent portions are concerned. Roots proceeding from the radicle of the embryo are chiefly subterranean. The roots springing from the different forms of scaly stem are almost all subterranean, and we shall not be far wrong if we estimate the roots of 70 per cent of all existing phanerogams as subterranean.

Aquatic or floating roots (*radices natantes*) spring laterally from floating stems and are generally arranged in clusters, more rarely singly, and are to a slight extent spirally twisted. They are developed both from stems whose foliage-leaves lie flat on the surface of the water, and also from the floating, leafless stem-structures which have been metamorphosed into phylloclades (*e.g.* in *Lemna polyrrhiza, gibba, minor*). In these plants the root-tips are also surrounded by water. If they come to lie on the slimy bottom in consequence of a fall in the water-level, they do not penetrate into it, nor do they enter into relations with the particles of mud. Marsh-plants, on the contrary, send their first roots right down into the mud, whilst those developed subsequently from the higher internodes are allowed to float in the water. The primary root produced from the seed of the Water Soldier (*Stratiotes aloides*) is embedded in mud, and is therefore really a subterranean root; after it has died off the whole plant rises up, remains oscillating below the surface of the water, and develops floating roots from its abbreviated, leafy stem; later the plant again sinks down, and the floating roots again become subterranean (*cf.* the account on p. 76). Conversely it often happens that subterranean roots become transformed into aquatic roots. In alders, willows, and elms growing on the sides of streams, extensive net-works of roots are often to be seen which have grown out from the slope of the bank and float in the water. Indeed, many terrestrial roots, strangely enough, exhibit a much more luxuriant growth in flowing water than in the ground, and it is well known that the roots of the above-named trees, when they have effected an

entrance into water-pipes, grow so extensively that in a short time the pipes are entirely blocked up and the water-flow in them interrupted. The net-works of roots taken out of these pipes resemble plexuses of hair, so abundantly are their tresses developed. Hyacinths and many other bulbous plants, and even various foliage-trees, as, for example, maples and horse-chestnuts, whose roots usually grow in the ground, can be reared with the best results if their roots are allowed to grow in water, provided that the water contains the necessary food-salts in adequate amounts.

Aërial roots (*radices aëreæ*) are developed on the periphery of the erect caudices of tree-ferns, and in great profusion on the stems of epiphytes, especially of aroids and orchids. In species of the tree-ferns *Todea* and *Dicksonia* the aërial roots are all very short but so numerous and crowded together that they form an actual mantle round the caudex. In orchids growing on the bark of old trees the aërial roots also arise in great numbers close together, but are always elongated and filamentous, and form manes, as shown, for example, in *Oncidium*, figured on p. 221. In other orchids, however, they may occur singly, and are then usually much thicker, fairly stiff, and curved sinuously in and out or spirally twisted as in the *Sarcanthus rostratus*, illustrated on p. 107. As already stated, in many aroids and orchids they appear arranged with great regularity, either singly or in pairs, opposite the points of insertion of the leaves on the stem. All these aërial roots are excellently adapted by their structure (described on p. 222) not only for the absorption of water and solutions of food-materials, but also for the condensation of aqueous vapour from the surrounding air. In most instances they are enveloped by a papery covering; more rarely they are thickly beset with so-called root-hairs, and then have a velvety appearance. Most of those with root-hairs are rusty brown in colour, whilst the others are white in dry air, and greenish in wet weather —in consequence of the abundant chlorophyll contained in the tissue below their papery envelope.

We must carefully distinguish these condensing aërial roots from such as, whilst springing from epigeal stems and surrounded by air, are unable to condense aqueous vapour or to absorb atmospheric water. These, on the other hand, grow down to the ground and must penetrate into it in order to obtain the water and food-salts they require. These root-structures are especially observed in climbing plants in which the lowest internodes have died, and which then no longer stand in direct connection with the soil. Their large foliage-leaves nevertheless require a much greater amount of water than could be obtained from the tree-trunks on which they support themselves. The large-leaved aroids illustrated on p. 365, whose cord-like roots, from 4 to 6 metres in length, descend to the ground, may be regarded as typical of this class. These forms are indeed called aërial roots, but if we adhere to the distinction given above, they would be more accurately regarded as a special class of subterranean roots. But since it has been repeatedly observed that the aërial roots of some orchids, when they come in contact with the ground, penetrate into it and assume the character of subterranean roots, the boundary

between subterranean and aërial roots vanishes, and, as in other similar cases, it becomes evident that all these classifications are but artificial.

Parasitic roots (*radices parasiticæ*) grow down into the living tissue of the host-plant and absorb from it the materials needed by them, and by the plant to which they belong, for further development. They are sometimes called *haustoria*. They are either wart-like, disc-shaped, or spherical in outline, or assume the form of sinkers; occasionally they remind one of a hyphal net-work. Sometimes they spring laterally from an epigeal, sometimes from an underground stem. They also frequently proceed as lateral members from underground roots. Their structure and various developments were so fully described on pp. 173–213 that we need only now refer to what was there stated.

Roots, whose especial province it is to maintain a plant in the position it has once assumed, may be distinguished as *clinging* and as *supporting* roots. Clinging roots (*radices adligantes*) really comprise all roots whose absorbent cells are so closely united with the substratum that a displacement can only be brought about by the exertion of considerable force. Even floating roots, inasmuch as they adhere to the water and so give a certain amount of stability to the whole plant, may be regarded as clinging roots. The duckweeds (*Lemna minor, polyrrhiza, gibba*), whose long, spirally-twisted, fascicled roots grow down into the water, are not easily moved by wind from the position they have taken up. Plants are of course still better fixed in the substratum by subterranean roots which adhere to the solid particles of the soil by means of their root-hairs. By this union of roots and earth-particles we get a compact mass, difficult to break up, and it is well enough known that loose soil may be solidified by plants possessing much-branched, wide-spreading roots, and that certain grasses are made use of to bind shifting sands together. When clinging roots are mentioned in plant descriptions, those in particular are referred to which firmly connect epigeal portions of stems to any support, as, for example, the short, climbing roots of the Ivy, or of *Tecoma radicans*, the much-branched roots which cover stones and the bark of trees with their net-works, the adherent roots of numerous species of *Bignonia* and *Cereus*, and the ribbon-like roots of certain tropical orchids which have fastened to the bark of trees,—especially those of *Phalænopsis Schilleriana*, described on p. 108; and finally the girdle-like roots of *Ficus* and *Wightia*, figured on p. 705.

Supporting roots, as their name implies, have the task of supporting the stems to which they belong. They are always visible above-ground, and assume the form of buttresses when they spring from erect trunks, of pillars when they belong to the projecting lateral branches of a stem. They may be conveniently divided into tabular, stilt-like, and columnar roots. Tabular roots (*radices parietiformes*) proceed from the lower part of an erect trunk, and have the form of tablets placed on end. They may also be compared to massive planks of wood used for fencing in roads. They radiate out in all directions and give to the approaches to the main trunk the appearance of short precipitous valleys which become gradually narrowed and terminate blindly in an acute angle. The tabular roots frequently resemble narrow

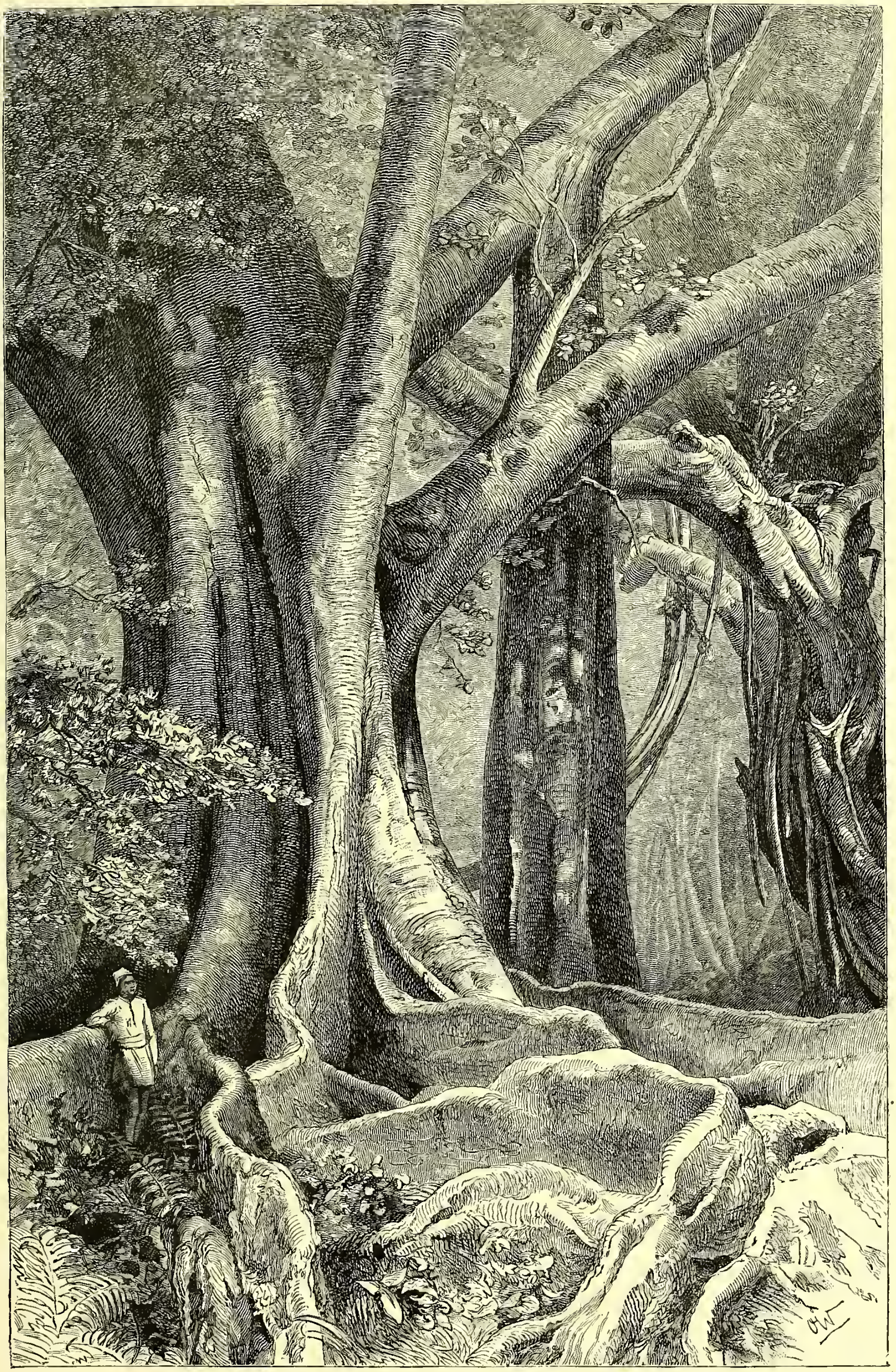

Fig. 185.—India-rubber Fig (*Ficus elastica*) and Banyan-tree (*Ficus Indica*).

buttresses, with regular radiating arrangement around the trunk, inclosing small niches, much sought after as hiding-places by various animals, and offering very acceptable holes to foxes, for instance. In point of fact, these roots are often called "buttress-roots". Tabular roots are a peculiarity of tropical trees with huge, heavy crowns. A particularly well-defined form is exhibited by the West Indian Cotton Tree (*Eriodendron caribæum*) and by the India-rubber Fig (*Ficus elastica*) belonging to tropical Asia, and yielding caoutchouc. The picture of this tree, drawn from nature by *Ransonnet*, fig. 185), gives us a very clear idea of these tabular or buttress-roots; the same figure, in the background to the right, also shows another species of *Ficus*, viz. the celebrated Banyan-tree (*Ficus Indica*), which will be described presently.

Stilt-like roots (*radices fulcrantes*) also arise in the same way from the erect or oblique main trunk, but they are cylindrical, and have the form of oblique props. Sometimes the oldest, lowest portion of the erect trunk thus supported dies away, or the disintegration may be continued some little distance up, so that only the upper part of the stem remains fresh and living. The first roots of mangrove seedlings (illustrated on p. 605), which penetrate the mud, have also the power of raising the trunk to which they belong up above the mire by their growth in length. These trunks then look as if they were on stilts, and are only connected with the ground by means of the roots. On page 758 we have a figure of the Screw Pine (*Pandanus*), and in fig. 187, of a species of mangrove, in both of which these odd root-structures are seen. They are also to be found in many other plants of the tropics, viz. in palms, Clusiaceæ, and fig-trees. In some clusias the stilt-roots are thicker than the stem they support, and in the mangroves, growing in crowded forests on the sea-shore, where they are exposed to the ebb and flow of the tide, they branch and fork continually, forming a tangled confusion, the strange appearance being heightened by the fact that all the root-branches and stems, up to the level of the water at high tide, are covered with an armoured coat of various molluscs and crustaceans.

Columnar roots (*radices columnares*) originate from horizontal or obliquely ascending branches of trees, and grow vertically down until they reach the ground. They then penetrate into it, unite with the soil, and thus form pillars on which the widely projecting boughs of the tree are supported. Trees whose erect trunks are supported by tabular roots and those which are provided with stilt-roots may at the same time develop columnar roots from their branches. One of the oblique branches of the India-rubber Fig, illustrated in the foreground of fig. 185, is seen to be supported by a huge pillar, which gets thicker towards the base, whilst the mangroves figured on pp. 605 and 759 also exhibit long, supporting roots passing down from the lower horizontal branches of the crown, which push in between the stilt-roots, and grow down into the mud. Not long ago these mangrove roots were thought to grow out of the fruits while these were yet hanging on the trees, and to grow lower and lower until finally they reached the swampy ground. It is, of course, true that the embryo grows out from the fruits while they are hanging

on the branches; but they become detached, as described on p. 603, as soon as they are from 30 to 50 cms. long, and falling with considerable velocity, bore into the mud by their lower thickened end. It never happens that one of these embryos *grows* down to the ground from the branch, and there is no doubt that the long roots extending from the crown of the tree down to the mud originate from the lower horizontal branches of the mangroves just like other columnar roots. Columnar roots are distinguished from the flexible, cord-like, aërial roots of aroids and other epiphytes (*cf.* p. 365) by their great resistance to bending and by their possession of a characteristic mechanical tissue, in consequence of which they have a totally different internal structure, which, however, will be described later on.

Perhaps the most imposing cases of development of columnar roots are exhibited by the Indian banyans (*Ficus nitida, Tsiela,* and many others), which are usually comprehended under the name *Ficus Indica,* one of which is illustrated in the background of fig. 185. To these also belongs the celebrated Asvhatta, the sacred Fig-tree of the Hindoo (*Ficus religiosa*), beneath the shade of which Buddha is said to have learned the vanity of existence and the mystery of the universe. In proportion as the boughs which project almost horizontally from the main trunk of this tree become stronger, and give rise to branches and increase in weight, they send out cylindrical roots which grow down to the ground, penetrate into the soil, strengthen themselves by lateral roots, and serve as supports for the branches in question. These columnar roots, which continue to grow in thickness, resemble erect stems, develop leafy branches, and not only function as supports, but also serve for the absorption and transmission of water and dissolved food-salts from the ground. Below the crown of one of these banyan-trees we might imagine ourselves in a spacious hall of which the roof is supported on pillars; and since the leafy covering of the crown is almost impervious to rain and sun, a weird twilight always pervades these halls even during the daytime. Tradition states that an army of 5000 men have encamped in the halls of a single banyan-tree. Near the village of Dena Pitya, in Ceylon, there stands an Asvhatta under whose shade a village of a hundred huts is established, and in a single banyan-tree 350 large and 3000 smaller columnar aërial roots have been counted. When left entirely to themselves the banyan-trees scarcely ever assume such gigantic proportions, because the ground under the crown is so dry and hard that the supporting props which grow down often fail to penetrate it and are unable to take root there; but in the trees held sacred by the Buddhists the rooting is assisted by conducting the roots descending from the branches through long bamboo tubes, and by breaking up and moistening the soil where they would penetrate into the ground.

The shape of roots differs materially according as to whether the plants to which they belong are annual, biennial, or perennial. Annual plants produce as many seeds as possible in the short period of vegetation allowed them, and provide the embryos within the seeds, which have to travel about the world, with the

Fig. 186.—The Screw Pine (*Pandanus utilis*). From a photograph.

Fig. 187.—Stilt-like and columnar roots of Mangroves.

reserves of food necessary for the founding of a new establishment. It would be of no use, and contrary to the economy of plants, if reserve materials were deposited in any other parts, say in the stem or roots, since these parts shrivel and dry up as soon as the seeds are dispersed, and the energy expended in the manufacture and storage of starch, fat, sugar, and other reserve food would be expended in vain. The roots of annual plants are therefore satisfied with delivering the necessary water and the required amount of food-salts to the plant during its short period of vegetation, and with providing a suitable attachment to the substratum; they waste no energy in founding subterranean reservoirs. In biennial and perennial plants it is quite otherwise. Biennial plants—as well-known examples of which may be taken the various roots used as vegetables, the Carrot (*Daucus Carota*), the Turnip (*Brassica Rapa rapacea*), and the Beet-root (*Beta vulgaris rapacca*)—develop during the first year a very short stem with foliage-leaves crowded in a rosette, and a thick, fleshy tap-root (*radix palaris*), or turnip-shaped root (*radix napiformis*). When vegetative activity recommences in the second year, an erect shoot with foliage and flowers is constructed at the expense or at any rate with the help of the materials stored up in the thickened root; fruits are produced from the flowers, and after the ripening of the seeds the whole shoot dies off together with the exhausted roots. In perennial plants the roots, when they serve for the reception of abundant reserve-materials, are usually considerably thickened; but in these plants it is the clustered root-fibres springing from the lower end of the underground part of the stem, after the primary root has died off, which undergo this development. When the thickening is symmetrical and fusiform, as in the Orpine (*Sedum Telephium*) and in the white-flowered *Orobus Pannonicus*, the roots are called fusiform (*radices grumosæ*); when they are swollen at intervals into knots, as in the Dropwort (*Spiræa Filipendula*), and in the yellow Day-lily (*Hemerocallis flava*), they are termed nodose (*radices nodosæ*). Many of our terrestrial orchids have two kinds of roots united in a fascicle, long cylindrical vermiform roots and short thick roots filled with reserve-materials which look very like tubers, and are called tuberous roots (*radices tuberosæ*). The Mediterranean flora and that of steppes, where in midsummer the vital activity of plants is much reduced, are particularly rich in plants whose roots are developed as storehouses for reserve materials. Plants of widely different families (e.g. *Ranunculus Neapolitanus, Centaurea napuligera, Valeriana tuberosa, Rumex tuberosus, Asphodelus albus*) there form thickened fascicled roots crowded with reserve-materials which pass through the dry season unharmed underground, and in the next period of vegetation supply the materials for the rapid construction of epigeal foliage and flowering shoots. These thickened bundles of roots are characteristic of the perennial, parasitic species of the genus *Pedicularis*. They serve for the storage of reserve foods, for the fixing of the plant, and for the absorption of nourishment, but the latter function is here carried on by means of suckers, which are developed at the end of the thickened fusiform fibres, and which attach themselves to the roots of the host plants in the manner described on p. 179.

It would naturally be expected that in accordance with the various tasks assigned to roots there should be a difference in the arrangement of cells and tissues, and that, especially, supporting roots which exhibit the greatest analogy with erect stems, and subterranean roots, which have so much in common with procumbent and subterranean stem-structures, should resemble them in internal structure. Columnar roots cannot really be distinguished from upright stems in their inner construction, and stilt-roots also present an arrangement of cells and vessels which often agrees much better with that of erect stems than of underground rhizomes. In *Fragræa obovata,* belonging to the Clusiaceæ, the cellular structure of the erect stem is only distinguishable from that of its supporting roots by the somewhat stronger development of the medulla and woody portion of the vascular bundles, but otherwise there is no sort of difference. The stilt-roots of the mangrove figured on p. 759 (*Rhizophora conjugata*) likewise show a stem-like internal structure. In the centre is a thick pith surrounded by numerous, conducting bundles, which together form a hollow cylinder, and are accompanied by mechanical tissue; further outwards come the cork, hypoderm, and a strongly-cuticularized epidermis—exactly the same arrangement required in an erect stem as a protection against bending. In these mangroves the strength is even increased by a peculiar tissue, viz. by so-called trichoblasts, peculiarly interlaced fusiform cells with very thick walls, which are so hard that even the sharpest knife will scarcely cut through them. Though these adult roots are structurally indistinguishable from stems, this is not usually true of them at early stages in their development. When young, and as yet unthickened, these roots, as a rule, possess an internal structure characteristic of roots in general.

In mangroves and in the earlier mentioned Clusiaceæ, the supporting roots are thick and widely spread, and form extensive foundations which entirely replace the comparatively weak trunk, so far as fixing on the substratum is concerned; they need especially to be protected against bending. A resistance to tension scarcely comes under consideration in these plants. It is quite otherwise in plants whose stilt-roots have to support a stem bearing an extensive and richly-leaved crown. The *Pandanus* figured on p. 758 may serve as a type of these. As soon as wind sways the massive crown and slender stem bearing it, the roots supporting the stem on every side have alternately to resist bending and strain. If the wind blows from the north, the supporting roots springing from the south side experience a longitudinal pressure as the stem inclines to the south, and are pressed and curved down like an arch, while the supporting roots springing from the north side are at the same time subjected to a powerful strain. When the wind sinks, the stem is again brought into its erect normal position by the elasticity of the south roots. The reverse is the case when the wind attacks the crown and stem from the south. This form of stilt-root must therefore be constructed so as to resist strain as well as bending, and accordingly in the aërial roots of *Pandanus* are formed two cylinders of mechanical tissue, an outer one which is formed by the hard bast of a peripheral ring of vascular bundles, resembling the arrangement

occurring in the majority of dicotyledons, and an inner which is formed of th hard bast of a ring of vascular bundles lying near the centre of the root. By th former the supporting roots are afforded the necessary resistance to bending, an by the latter the corresponding resistance to strain.

The stilt-roots springing from the lowest nodes of maize-plants are adapte to this double function just as are those of *Pandanus*. Here also are two cylinder of mechanical tissue. The outer one, situated in the cortex, consists merely o hard bast and provides a resistance to bending, while the inner, in connection wit the conducting bundles, furnishes a resistance to strain. In the stilt-roots at th base of the maize-stem there is, however, a central pith or wide medullary cavit which is wanting in the roots of *Pandanus*.

Clinging roots adhering to the bark of trees, stones, or some other hard sub stratum, as well as the many forms of subterranean roots, are not required to resis bending, and in them there is none of the mechanical tissue which would b necessary for this resistance. On the other hand, these roots are unavoidabl subject to a severe strain from the pulling exerted by the stem and branches a they sway to and fro. For a cylindrical body which has to resist a powerfu longitudinal strain there is no better contrivance than the fusion of the resistin elements into a compact mass in the axis of the cylinder, and this arrangement i actually met with in clinging and subterranean roots. The conducting bundle and the adjoining mechanical tissue form a single central strand in the cylindrica root, and the typical form of a subterranean root is a cylindrical body of tissu which has no central pith and no hard bast cylinder near the circumference, bu whose vascular bundles are so crowded towards the axis that they form there single, thick strand or "central cylinder".

Roots embedded in the ground are of course exposed to a lateral pressure fron their surroundings, and care must be taken that the functions of the conductin bundles are not disturbed by this pressure, that the transmission is not interrupte or even entirely stopped. This is effected by padding the central strand jus described, that is, by surrounding it with a mantle of parenchymatous cells. Th thickness of this coat varies according to the extent of the lateral pressure, an when the roots are subjected to very great pressure, the walls of the parenchyma tous cells are even thickened in a corresponding degree.

Reserve-materials may also be deposited in this parenchymatous mantle. I biennial and perennial roots the tissue surrounding the sap-conducting and strain resisting strand is not only thickened so as to give the necessary support agains pressure, but also provides a place for starch, fat, sugar and other supplies whic are to be consumed in the next period of vegetation.

Naturally these soft tissues, often filled with reserve-food, are an attraction t diverse animals living underground, and the establishment of such a storehous renders a corresponding protection against the attacks of mice and insect-larva necessary. Though the protective agents and weapons by which the green foliag and flowers, and fruit are preserved from the ravages of animals would not serv

here, still, by the development of poisonous and disagreeable substances, the subterranean, burrowing insects are, as far as possible, kept away. It is well known that roots are particularly rich in poisonous alkaloids, in resins which are repulsive to animals, in bitter substances and the like; these parts of plants are well known as providing many drugs of the pharmacopeia. These do not indeed afford an infallible protection against all attacks from animals, but that a partial safeguard at least is obtained by the storing up of certain materials seems very probable by the following observations. The field-mice in a garden at Innsbruck once caused great havoc under the winter coat of snow, and various roots were gnawed by them; but the roots and root-stock of the Soapwort *Saponaria officinalis*), containing quantities of poisonous saponin, were always eft untouched by them. The bitter roots of gentians (*Gentiana punctata, lutea, Pannonica*), which are very rich in reserve-foods, and which grow in deep alpine neadows riddled by mice, were never seen to be attacked by a single animal. This was also the case with the thick tap-roots of the poisonous monkshood, the nassive roots of rhubarb-plants and of many Umbelliferæ, which are all abundantly upplied with starch and other food-stuffs, and therefore would afford an excellent ood for herbivorous animals under stress of hunger.

When the parenchymatous tissue surrounding the central strand of the conlucting bundles in subterranean roots serves not only as an agent for protecting gainst lateral pressure, but also for the storing up of food-materials, and in ddition possesses contrivances for warding off voracious animals, the structure of he roots is much more complicated than in cases where it affords protection against iteral pressure alone. There are also very many different developments of parnchymatous tissue on the periphery of subterranean roots in accordance with the arious demands necessitated by the conditions of the habitat and the peculiar iode of life of the species. In aquatic roots the need for abundant ventilation has lso to be considered, and the storage of reserve-foods in these organs must be voided since the increase in weight, due to the massing of reserve-food, might raw the floating water-plant down into the water at an unsuitable time.

A storage of food-materials in the special tissue developed at the growing rootp, and known as the *root-cap*, would also be unsuitable. In subterranean roots ie root-cap only protects the delicate dividing and multiplying cells at the growing id. The pressure to which these continually dividing cells are exposed in their enetration into the ground is much greater than that operating on the fully rmed parts behind the root-tip. The growing point of the root has to push on ie side hard grains of sand and other particles of earth, and to make a hole like a round-auger in which later on the fully developed root can take up its position. he root-cap may be compared to a shield which is formed by the growing and ierefore advancing cells in the direction required, these constantly pushing it in ont of them. This shield is always being supplemented and renewed by the owing tissue. The half of the root-cap adjoining the growing tissue consists of gular, closely-fitting cells; the outer half, directed towards the soil, consists of

rounded, loosely-fitting cells, and on this outer side of the root-cap the cells are also seen to be partially separated and torn off. As the outer cell-layers are rubbed away by the advance of the root, and by unavoidable contact with the surrounding soil, new cells are always being pushed forward from within, and in this way the loss is made good, and the shield continually repaired.

Obviously, aquatic roots do not require a shield of this kind at their apex, and in aërial roots, at least in the form described, it would likewise be superfluous. Even roots which penetrate into mud do not require it. Accordingly many water-plants and the marsh-inhabiting mangroves do not develop a cap at their root-tip. The root-cap is also entirely absent in parasitic plants which it would only hinder from penetrating into the tissue of the host-plants.

DEFINITION OF THE ROOT.

In the preceding pages we have continually spoken of roots, although we have not yet defined technically what a root is, and now, contrary to the usual custom in scientific works, the definition of this organ has to come not at the beginning but in the middle of the chapter. This alteration in position has been caused by the necessity of establishing the definition on some peculiarities in the external and internal structure of roots, with which we could not suppose all readers to be familiar, and which therefore had to be described beforehand as far as required.

But many readers will ask if any definition is required, if everyone does not know without it what the root of a plant is, and how it can be distinguished from a stem and leaves? The case is exactly parallel with that of the leaf. Every one who is not a botanist thinks he knows what is meant when he hears the word "leaf", and cannot conceal his astonishment or possibly his smile when he is informed that scientific men are not agreed about such a simple question, and that they write violent polemics upon this question. To the impartial reader debates as to whether a certain part of a plant is to be regarded as a root or not doubtless appear hypercritical and a pedantic splitting of hairs, and with regard to many of the discussions I would hardly venture to deny the justice of his position. The savant who constructs for himself the picture of an ideal or primitive plant from a sometimes larger, sometimes smaller number of single observations, who finds out how the individual parts were situated in their succession as to time, and in their mutual relations in space, and who distinguishes and defines the various parts accordingly, is indeed very easily tempted to take the abstract ideal he has created as a standard for the whole vegetable kingdom. From his point of view, obtained by the consideration and comparison of so many individual cases, all forms are arranged and explained, everything must fit into the now firmly established groundwork, and where it will not coincide, he talks of exceptions, forgetting that in such a case exceptions are not permissible, but are rather a proof of inadequate generalization from the single cases observed.

In the comprehension of the results of general comparative studies of this kind

into the configuration of plants, it is a matter of great import how the definitions of the individual parts and members of the plant are formulated, and whether the author lays particular stress on this or that characteristic. Suppose that some observer holds the opinion that the presence or absence of the root-cap affords an important distinction between a root and stem; then he would speak of the supports of mangrove-trunks as lateral stems which grow downwards; another, who lays particular weight on the fact that roots produce no leaves behind their growing points, would, on the contrary, declare the supports of the mangrove-trunk to be roots devoid of root-caps. It would be the same with the contradictory explanations and different appellations which would be given to the supports of Clusiaceæ and figs, to the fixing and absorbent apparatus of Mistletoe which penetrate into the host-plant, and to so many other hypogeal and epigeal parts of the plant-body.

These examples will suffice to show how a conflict may arise over such an apparently simple thing, how easily the investigators into the region of the speculative science of form may become one-sided, what great difficulties are to be encountered in formulating a definition, and how in particular a hasty generalization must be avoided about characteristics which it is not at all certain are really to be met with universally. Every definition is dependent upon the extent of our knowledge at the time; it may not hold good as our experience widens, and therefore has only a relative value.

From the standpoint of our present knowledge, however, the following may be taken relatively as the best definition:—A root is a body of tissue provided with vascular bundles, which originates from an older, previously-existing part of the plant; its growth is not limited, and it never directly gives rise to leaves.

In connection with this definition, some remarks may be made here by which many relations between the root and other parts of the plant will be elucidated. First it should be noted that in the above definition the youngest developmental stage, viz. the embryo, is included under the term "plant". It has further to be explained why the characteristic which is first thought of in non-botanical circles, when speaking of roots, viz. their power of deriving fluid nourishment from another body, has not been mentioned in the above definition. It is perfectly correct to say that an absorption of fluids is generally observed in roots, but in reality it is only the root-hairs proceeding from the roots which perform this task, and these absorbent cells are known to be also developed on stems and leaves. The cotyledon extended from the seed of the Bulrush (*Typha*), penetrates into the soil with absorbent cells. The cavities of the green leaf-structures in insectivorous plants are also abundantly provided with them, and special absorbent cells are developed on the green leaves of many saxifrages, tamarisks, and so forth; whilst in those marsh-plants, the leaves of which float partly on the surface of the water and are partly submerged, the epidermal cells also function as absorbent cells. In many aquatic plants (e.g. *Hottonia, Ceratophyllum, Naias*) absorption is only carried on by means of the epidermal cells of the foliage-leaves, and no trace of roots is to be found in them. Their foliage-leaves, however, remind one very much of root-

structures, and in a floating water fern (*Salvinia natans, cf.* vol. ii. fig. 380) the submerged leaves have the greatest resemblance to roots in shape and colour. In such cases, though we can say that the leaves are metamorphosed into absorbent organs, we cannot assert that they have become roots. This applies also to plants whose underground stems are provided with absorbent cells (*e.g. Bartsia, Epipogium, Corallorrhiza*), or whose stem-structures, submerged in water, are furnished with epidermal cells functioning as root-hairs (e.g. *Lemna trisulca*). In these plants the stem-structures are indeed metamorphosed into absorbent organs, but they are never transformed into roots.

We are accustomed to think of the roots of plants as organs with white, yellow, red, brown, or black, but never green, colour, because as a matter of fact by far the greater number are devoid of chlorophyll. But there are plants whose roots do contain chlorophyll, *e.g.* those of *Lemna minor*, and various aroids and orchids. In orchids with aërial roots but no green foliage-leaves, the green roots must take on the formation of organic compounds from food-gases in sunlight, that is, the function which is performed by the foliage-leaves in so many other cases. We should, therefore, be as little justified in bringing forward the absence of chlorophyll as a characteristic feature of roots as in saying that the roots had become changed into green leaves. The roots of the orchids mentioned have indeed become transformed into assimilating organs, but they remain roots nevertheless.

It was formerly thought that roots and stems could be distinguished, the former by their inability to develop buds, and the latter by their power of forming them. But although this difference is actually observed in most instances, it cannot be applied universally. The roots in many plants develop buds which unfold into leafy shoots, and not merely lateral, but terminal buds also. When this happens it looks as if the root were continued directly into a leafy shoot, and this occurrence has led to the mistaken idea that the root-tip may become metamorphosed into a leafy stem.

Finally we have to consider the difference in the mode of origin of roots and stems. It cannot be denied that the points of origin of stem-structures are usually arranged geometrically, while roots only exhibit such an arrangement in rare cases. But we must again insert the words "usually" and "rare", for here too a universal distinction does not exist. The stem-structures springing from the underground roots of the Aspen (*Populus tremula*), and from old trunks of the Black Poplar (*Populus nigra*) make their appearance quite irregularly, whilst, on the other hand, the roots of many aroids originate with the same regularity as leaves and the lateral shoots arising from the axils. In most cases the root proceeds from a group of cells in the interior of a stem or older root, and it used to be thought that this constituted a difference between roots, and stems and leaves, since the latter arise from cells near the surface of the tissue-body which bears them. But aquatic roots, *e.g.* those of *Ruppia* and *Zannichellia*, also proceed from cells near the surface of the stem, and in the same way roots arise from the epidermal cells of the leaves of the Cuckoo Flower (*Cardamine pratensis*), and from

the parenchyma lying immediately below the epidermis, so that this again does not furnish a universal distinction.

But although all those characters, which have been used in turn to characterize the root, cannot be thus employed because they have not a universal value, yet one distinguishing feature always remains, viz. that leaves are never produced from root-tissues, and the greatest stress is to be laid on this point. After weighing everything carefully we come to the conclusion that the plant, and even its youngest developmental stage, the embryo, begins with a stem, which develops leaves and roots. Stems, leaves, and roots may perform widely different functions, may shape themselves accordingly, and may be metamorphosed into widely different organs. A plant is comparable to a crustacean which is divided into a body and appendages. The appendages in most cases serve as organs for locomotion, grasping, and clinging, but are sometimes also metamorphosed into respiratory organs, egg-carriers, &c.

REMARKABLE PROPERTIES OF ROOTS.

The small stem-structures which proceed from germinating orchid-seeds behave very differently according to the nature of their germinating bed. From the small tubercles of species growing as epiphytes on the bark of trees arise, first of all, hair-like absorbent cells which adhere to the substratum; then roots make their appearance, which also unite firmly with the bark, though their superficial cells are not able to penetrate into it. The small tubercles of the terrestrial orchids, which inhabit the meadows and the humus of the forest soil, develop roots which grow down into the ground and direct their growing tips towards the centre of the earth. In this way they draw the stem-structure from which they originate down with them, and thus the tuberous stem in two years' time comes to lie 6–10 cm. below that point in the meadow where the seed actually germinated. The same thing happens with the embryos of many biennial and perennial plants, especially of those whose underground roots and stems are subsequently used as storehouses for reserve materials, *e.g.* in Carrots, Evening Primroses, in the Monkshood, Meadow Clover, Vincetoxicum, Dog's Mercury, Martagon Lily, Bulbous Crowfoot (*Daucus, Œnothera, Aconitum, Trifolium pratense, Cynanchum Vincetoxicum, Mercurialis perennis, Lilium Martagon, Ranunculus bulbosus*), and many others. In these plants also the embryonic stem is drawn more or less deeply under the ground, and the scarred point of insertion of the cotyledons is not infrequently found to be several centimetres lower down that it was at the time of their withdrawal from the integument of the seed.

Many roots arising later on from procumbent and from erect or twining and climbing leafy stems have the power of exercising a pull on their stem. The roots springing from the stem nodes of runners, *e.g.* from those of strawberry plants, draw the nodes a centimetre below the ground. This is also the case with the long roots proceeding from the stems of perennial primulas. When these primulas

settle in the clefts and crevices of perpendicular rock faces, a phenomenon is produced by this down-drawing which surprises anyone noticing it for the first time, appearing at first quite inexplicable. The thick stems of these primulas (e.g. *Primula Auricula, Clusiana, hirsuta*) are terminated by a rosette of foliage-leaves; these turn yellow, and dry up in the autumn, and a new rosette is laid down in the axil of one of them for the next year. Although the leaves of the rosettes stand close above one another, the portion of the stem clothed by them is quite a centimetre long, and the annual increase undergone by the stem which grows towards the light is also a centimetre. The increase during ten years would amount to 10 cm., and it would be expected that the rosette of the tenth year would be about 10 cm. above the level where stood the first year's rosette. But, strange to say, the rosettes of all the succeeding years always remain at the same place, that is, they always cling to the rocky edges of the crevice or cleft in which the stock is rooted. The explanation of the phenomenon is that the roots springing from the rosette-bearing stem draw it down every year about a centimetre into the soil or crevice filled with humus. But naturally this can only occur if the lower end of the stem annually dies off and decays to a corresponding extent, and this is what actually happens. In rocky clefts which are not well adapted to this process the primulas grow badly, and their stems project above the edges of the crevice; ultimately the entire plant falls into a slow decline and no longer blossoms, but perishes in a few years. The knowledge of their peculiar mode of growth is therefore of some importance in the cultivation of these primulas, since care can be taken to plant them so that the stems can be annually drawn a certain amount into the soil by the roots. It is of course needless to mention that many other plants beside primulas, rooted in crevices of rock, behave in the same way, e.g. *Phyteuma comosum, Gentiana Clusiana, Campanula Zoisii, Paederota Ageria.*

The ends of branches of many species of bramble are drawn under the ground in a very peculiar way. One of these species, *Rubus bifrons,* is represented in fig. 188, where the roots and the ends of the branches drawn under the soil by them are rendered evident, the earth in the foreground being removed as if dug away by a spade. *Rubus bifrons* develops strong five-ridged shoots beset with reversed prickles; they at first grow directly upwards, but towards autumn hang in broad curves, so that their tips approach the ground. Before they have reached the soil, however, small scale-like protuberances, looking like stunted leaves, are to be noticed arising near the tip; these are the commencements of roots. When the apex of the branch at length trails on the ground the protuberances, now in contact with the soil, elongate into roots which penetrate the ground. They lengthen very rapidly, sending out numerous lateral roots, and in a short time an extensive subterranean root-system is the result. But the apex of the branch which serves as a starting-point for these roots, and which is now considerably thickened, has also come under the ground. It has been drawn down by the roots, and is now embedded in the soil. In the following spring, sometimes even

in the autumn in which the rooting has taken place, this branch apex, nourished by its roots, grows up into a shoot, which again appears above the ground. The

Fig. 188.—Bramble-bush in which the branches have taken root.

old branch, however, which had arched down to the soil, and whose apex had been drawn into the ground by the roots, dies off sooner or later, consequently a new, independent plant results from this action.

It has been shown that where stems are drawn into the ground, it is by means of the roots. After the growth in length of a root is completed, it shortens, in some instances only 2–3 per cent, in other cases as much as 20–30 per cent, *i.e.* almost a third of its entire length. The shortening depends upon alterations in the turgidity of the cells connected with an absorption of water. While the cells of that portion of the root which is still growing elongate by increased turgescence, those of the fully-formed root become shorter and broader in consequence of the increase in their turgidity. The parenchymatous cells in fully-formed roots become broader at the expense of their length in consequence of the increased turgescence produced by the absorption of water, and the natural result is a shortening of the whole tissue-body. This contraction of the mature root-portion exerts a tension on both ends. At the lower end of the fully-formed part of the root is the still immature portion growing downwards, whilst at the upper end that part of the stem from which the root originated. Above the downwardly-directed point the immature part of the root is equipped with hair-like absorbent cells, and these are closely united to the surrounding soil. In this way a resistance is afforded which the strain of the contracting part of the root cannot overcome. And since, as already stated, the cells at the growing end of the root are lengthened by turgescence, the tissue is extended, and the root-tip, in spite of the strain operating from above, continues to penetrate into the ground. The strain, therefore, has no effect in this direction. But it is otherwise with the pull exercised on the stem by this contracting of the root. There is no powerful resistance here to be overcome, and consequently the part of the stem in question, whether the hypocotyl of the embryo, the end of the epicotyl, or a node from the middle or end of the leafy foliage-stem, is drawn down into the soil.

This remarkable planting of course only occurs where the roots grow down vertically into the ground, and as remarked, it is most noticeably observed in species whose subterranean stem and root-structures store up reserve materials. Roots which run horizontally below the surface of the ground are not adapted to influence the stem in the manner indicated. On the contrary, in certain circumstances, these are able to effect an elevation of the stem. This happens especially in trees with thick woody roots, *e.g.* in pines and firs, oaks and chestnuts, and is to be explained in the following simple way. The first embryonic root growing down vertically into the ground soon dies off, or its development, especially its increase in length, is greatly retarded, and much more vigorous roots develop from it, or from the lowest part of the erect hypocotyl. These spread out in a horizontal direction under the surface of the ground. They usually radiate out in all directions forming a whorl at the base of the erect stem, as can be plainly seen in pines uprooted by a devastating storm. These horizontal roots at first have only a slight thickness, but their diameter increases with age, and the successive layers of wood in them form annual rings, just as in stems. Now these subterranean roots, in addition to resisting the pressure of the surrounding soil, actually exercise a considerable lateral pressure

by their growth in thickness. In consequence of this the soil below the cylindrical, horizontal root becomes compressed, but that above it is raised and burst open. The thick, woody root gradually becomes visible on the surface, and is entirely stripped of earth on the upper side. The axis of the horizontal root never again assumes the position of earlier years; then the roots were only a few millimetres thick, but now they have attained to a diameter of 20–30 centimetres, and the root-axis has been shifted upwards through almost half its diameter, *i.e.* through 10–15 centimetres. The erect trunk, which is firmly united to the horizontal roots in the way just described, is, of course, raised up to the same extent. In this manner may be explained the peculiar appearance so frequently to be seen in our pine and oak forests—the appearance of huge tree-trunks with thick woody roots springing from their base which are quite devoid of earth on their upper sides, and run, half underground, in snake-like coils into the forest ground.

The elevation of stems by means of roots is more striking in tropical mangroves even than in our native trees. After the seedling has fallen from the tree and bored its way into the mud, protuberances arise on the circumference of its lower third which develop into roots directed obliquely downwards. Even in a few months the buried plant is raised up a little above the mud by the lengthening of these roots, so as now to look as if it were supported on stilts.

It has been repeatedly mentioned that the primary roots of the embryo originate from places on the hypocotyl which have been determined beforehand. So also does the origin of roots on many rhizomes, runners, and on climbing stems seem to be precisely determined, and to be quite independent of external influences. For example, the primary root of mustard and numerous other plants is developed under all circumstances from one pole of the hypocotyl. The runners of strawberry plants and of the Creeping Crowfoot (*Fragaria vesca* and *Ranunculus repens*) develop, without any external stimulus, a group of from two to five root-protuberances on the stem-nodes, and the bramble branches, described above, curve like arches to the ground, forming several root-prominences at definite spots near the apex before they have reached it, in order that they may take root in the soil. In many epiphytic aroids and orchids the places of origin of the roots are arranged as symmetrically round the stem as are those of leaves, and many other examples might be cited from which it follows that the position of part of the roots is definitely fixed beforehand, being based upon the specific constitution of the protoplasm of the species in question. But as well as the roots developing in the manner indicated in definite positions, others are formed which require for their development a special stimulus from outside, whose place of origin is not determined beforehand, but is first fixed by some external agent. To this category belong the roots arising from the nodes of shrubs which have been battered down on the ground, and from stems coming in contact with damp objects, as well as those which proceed from foliage-leaves, and, finally, the wart-like roots of parasites known as haustoria. When shrubs

with erect stems and thick stem-nodes, *e.g.* the various species of *Galeopsis* or *Polygonum*, are extended flat on the ground from some accidental cause, only a part of the stem rises up again after a time by a right-angled bend at one of the nodes, the part next the free apex rising up, while the part nearest the attachment remains prostrate on the ground. Contact with the soil acts as a stimulus to the formation of roots on this latter portion, and they are produced abundantly near the node from the knee-shaped bent portion, and penetrate into the ground, functioning as absorbent and fixing organs. These shrubby plants would not have developed any roots on their stem-nodes had they not met with the accident and so been stretched on the ground.

Cut branches of willow placed in water, wet sand, moistened soil, or moss, develop roots in about a week at the place where they are in contact with the water or damp objects mentioned; roots which are equally useful either as absorbent or fixing organs. If the branches had not been cut off or treated in this way, no roots would have been formed on them. These willow branches may be taken as a type of the shoots of a great number of plants which all readily develop roots from the stem when placed in damp surroundings. The propagation of plants by cuttings, so often performed by gardeners, depends upon the fact that when branches are cut off from a plant and placed in damp sand they "strike root" in it, *i.e.* they send out roots from the part of the stem situated in the sandy soil. Contact with damp earth operates as an incitement to the formation of roots in the aërial, cord-like roots of the aroids figured on p. 365, just as in these cuttings. The aërial roots descending from the stems of these aroids do not develop absorbent, lateral roots until they reach the soil; but they have scarcely come into contact with it when numbers of lateral roots arise which penetrate into the ground where they can suck up fluid nourishment. In the root-forming leaves of species of pepper, of begonias, and of the cuckoo flower, contact with damp soil stimulates the production of roots—in places, too, where no roots would have been formed without this contact. If a pepper or begonia leaf is cut in pieces, and each piece laid on damp sand and so pressed down that the veins projecting from the lower side are embedded in the sand, roots will grow out of the parenchyma adjoining the veins, and turn downwards, while above they develop a tissue-body which turns upwards and becomes a leafy shoot, being provided with food by the roots. Long roots arise from the cellular tissue at the base of the stalk of rank ivy-leaves placed in wet sand or in water, which is never known to happen when the ivy-leaves are growing freely in the air. We must not omit to mention here the roots of parasitic plants which attach themselves to the living tissue of other plants as so-called haustoria; these only arise in the parts of the parasite which come directly into contact with the succulent roots of the living host-plants.

The benefit which plants derive from the formation of these roots is easily perceived. In the stems of the prostrated shrubs the conduction of fluid food from the ground is, no doubt, restricted and imperilled, and therefore it is important that the part of the shoot again rising from the ground should be provided with special

roots at the node where the knee-shaped bending takes place, in order to conduct the absorbed nourishment directly to the foliage-leaves on the upper part of the shoot. The actual existence of the part of the plant in question depends upon the formation of such roots in the other cases enumerated above. The cut branches of willows, the cut-up foliage of begonias, the ivy-leaves torn from their stem, &c., would all die if they did not provide themselves with roots. But although it is easy enough to perceive the benefit ensuing from this kind of root-formation, it is very difficult to explain how the mechanical impulse brings about this new production. It has been shown in all these instances cited that contact with a foreign body is an important factor, but it is very puzzling to understand how the deeper cell-layers are stimulated to develop roots by the contact of the epidermis with damp earth, water, and the like, and we must content ourselves with saying that the contact acts as a stimulus, which, when transmitted to the deeper layers of cells, stirs them up to construct roots as a deliverance from death. The explanation is still more difficult in cases where the cut parts of the plant develop roots to preserve their life, even without contact with a foreign body. Such a case has been considered earlier (on p. 89), when it was shown that on cut shoots of various species of stonecrop (e.g. *Sedum reflexum*, *Boloniense*, *elegans*), which are hung in the air by a thread, roots will develop from the internodes between the foliage-leaves in places where no roots would normally have arisen. They grow down and elongate until their tips come in contact with some solid body. Here no stimulus could have acted on the epidermis; the pendent shoots stand in no relation to the surrounding air other than obtained whilst they were still united to the rooted plant, *i.e.* before they were cut off. The stimulus to root-formation must, therefore, be referred to the separation of the shoot from the plant. We must not, however, imagine the action to be merely mechanical, but must be content with stating that the living shoot hanging in the air can only save itself from death by developing these roots.

To the most remarkable vital phenomena of plants belong also the various bendings, curvatures, and other movements performed by growing roots. Apparently every root tries to reach a definite goal, towards which it directs its way, endeavouring to obtain the advantages offered by it with as little expenditure as possible. The goal which growing roots strive after is the same for all, viz. the place in the nourishing substratum best adapted to them. The primary roots of plants settled on the bark of trees as epiphytes or parasites direct their tips towards the axis of the branch of the tree in question, land plants on the other hand, towards the centre of the earth, and the primary roots proceeding from seeds lying at the bottom of still water sometimes direct themselves upwards and grow at the commencement of their development towards the surface of the water. The road to be traversed by the succeeding roots, from whatever part of the plant they may have sprung, is apparently not so clearly determined; but on a closer examination it is found that they too strive to attain to places where fluid nourishment abounds, and where they can obtain a firm hold. The

soil is made up of alternating places containing a larger and a smaller amount of food-salts, and places which either retain water badly or well. In one place are situated nests of humus, in another sharp-edged stones, and it is only natural that these inequalities and obstacles in the path pursued by the roots should not be without effect on them. As a matter of fact manifold contrivances are met with for preventing the roots from, so to speak, blindly passing by favourable places in the soil without making proper use of them. The fact that the tips of many roots describe oscillations or nutations, not unlike those which are observed in twining stems and in certain creepers, is an instance of such adaptation. Roots growing in soil are of course much more restricted in their movements by the pressure of their environment than are the structures which circle round in the air, but in the main the principle is the same in both cases. The path travelled by the point of the growing root is most accurately depicted by a spiral line, and the most important advantage obtained by following such a path lies in the contact of the growing root with as large a portion of the soil as possible. A root growing in a straight line would not touch half as many points as that following a spiral, and since the likelihood that all the favourable spots will not be left on one side increases with the number of points of contact, the spiral movement of the roots may without hesitation be regarded as a contrivance for discovering the best sources of food in the soil. We must, of course, not undervalue various other advantages which are also obtained in this way, in particular, the greater ease with which roots following a spiral line can bore their way into the soil, and the better hold they obtain.

Although the root follows a spiral line in its growth, it may nevertheless maintain a straight direction on the whole; this is actually the case in water and in a homogeneous and uniformly moistened soil. In soil differently constituted and unequally moistened, however, a diversion takes place away from the side where the conditions are unfavourable to the root. This swerving may be caused by cold, dryness, by chemical conditions of the soil, and by pressure and injuries.

It is well known that in the far north the ground remains always frozen below a slight depth. During the short summer only the superficial strata are thawed, but below this the "perpetual ice" stretches to an immeasurable extent. A relatively abundant vegetation develops on the thawed strata under the warm rays of the sun, and in North America not only shrubs and low bushes but also colonies of huge fir-trees grow up. The roots of these plants penetrate straight downwards and grow towards the centre of the earth; but as soon as they come into the neighbourhood of the ice they bend aside, curve round, and continue theii path only in the thawed stratum. The diversion is usually so striking that the diverted portion is sometimes actually at right angles to the older part which grew vertically downwards.

The same thing happens when the soil is moist in some parts and dry in others. Here again the growing roots seem to be repelled by the dry, inhospitable layers of soil, and turn towards the neighbouring moister region. This phenomenon has been

termed *hydrotropism.* It frequently happens in mountainous districts that after heavy downpours of rain the overflowing streams tear deep furrows in the adjoining steep forest lands, and root up the ground, throwing everything into confusion and depositing below on the valley-floor a mass of detritus or rubbish. Usually numerous organic bodies, blocks of wood, pieces of turf, leaves, fir-cones, and the like are torn away by these turbulent streams with the stones and sand, and the deposit is therefore studded with nests and strips of humus which owe their origin to the organic fragments mentioned. Seeds of various plants from the neighbouring forest are swept into the rubbish heap, and among them those which only flourish well in the damp humus of forest soil. These seeds germinate, and their roots penetrate downwards; many perish at once in the inhospitable soil, but others grow excellently, sending up a vigorous stem and unfolding foliage and flowers. When these well-grown plants are dug up in order to see the relation of their roots to their immediate environment, it at once becomes evident that the roots in their downward progress have curved towards the nests and veins of humus. They exhibit the most wonderful twists and bends, and look as if they had actually been attracted by the humus deposits. Without quite excluding the possibility of a chemical attraction, we must regard the aversion of the roots to dryness as the chief cause of the bending. The masses of humus embedded in sand and rubbish retain moisture like a sponge, and when the adjoining sand-strata have been for long dried up the dark nests and strips still retain their saturated condition. When a root shunning the dryness turns away from the sand, and in continuing its growth comes to a deposit of humus rich in water, it finds there no inducement to continue bending, and so grows straight through the region of the damp layer. When in its further growth it emerges from the ball of humus and enters the dry sand, it of course again bends and curves round the ball of humus, or wheels round in a half circle so as to return to the moist dark clump which is situated like an oasis in the dry desert of sand.

It is obvious that larger pebbles which cannot be displaced by growing roots must cause a swerving; the root whose tip is in contact with the hard stone bends sideways and evades the insurmountable obstacle lying in its path. A very noticeable bend ensues when the growing root is injured on one side of its tip, or is so fastened to some foreign object that the cells at the place of contact are damaged. It then bends away from the injured or attached side and assumes a divergent course.

In many cases it might be thought that the roots were not repelled by the unfavourable places in the soil, but were attracted by the favourable places, and, as already stated, the possibility of an attraction, a mutual action of the sap of the root and the materials contained in the places in question in the soil, which might find expression in a movement of the growing root-end, is not entirely excluded, although it has not hitherto been demonstrated with certainty.

The circling, that is, the spiral movement of the growing root, has been explained in various ways. One view was that the cylindrical body of the root may be

divided up into longitudinal strips, all of which were supposed not to grow at the same time or to an equal extent, but rather that the wave of stronger growth continually passes from one strip to the next one. This movement, however, like that of twining stems is probably an alternate bending towards the different radii of a circle drawn round the root, and since it is combined with an elongation of the part of the root in question, the growing root-end describes a spiral line.

The bend caused by the diversion of the root is either produced by a one-sided contraction, or by a one-sided elongation. Since the bend occurs in the growing portion of the root, a more vigorous growth on one side may be regarded as the immediate cause of the bend, and every impetus which would promote such unilateral growth would also cause a bending. The bending of roots which shun dry places may perhaps be referred to a withdrawal of water from one side of the root-tip. Thus if the root lies imbedded between a damp and a dry layer, that side which abuts on the dry stratum will transpire more actively than the other, and it has been suggested that this active transpiration in some way promotes an increased growth in length in that half, and in consequence of this unilateral elongation on one side, the other half, adjoining the damp layer, will become concave.

The idea that the curvature is not produced directly in the place where the external stimulus operates, but in the growing region lying behind the stimulated root-tip, is much more interesting than these purely mechanical explanations. According to this view the stimulus is transmitted as in the leaves of the Sundew, Fly-trap, Aldrovanda, sensitive plants, and many other cases. The active stimuli may be afforded by pressure, cold, dryness, and probably chemical conditions also. Gravity, too, may be looked upon as a stimulus, indeed as one which influences the direction of growth. It is believed that gravity acts on the root-tip as a stimulus to growth and that this stimulus is conveyed to the growing region behind, and that in consequence the primary roots grow down towards the centre of the earth. But as primary roots are able to penetrate into mercury, and to bore through paper, in their downward growth, something more than mere weight operates, since this would not be the case if the roots were influenced by gravity alone.

The part of the growing root most sensitive to stimuli is—so far as experimental evidence points—the tip, and the phenomena which are exhibited in consequence of its great sensitiveness are so astounding that Darwin compared the root-tip to the brain of lower animals. He writes, "it is hardly an exaggeration to say that the tip of the radicle thus endowed, and having the power of directing the movements of the adjoining parts, acts like the brain of one of the lower animals; the brain being seated within the anterior end of the body, receiving impressions from the sense-organs, and directing the several movements".

Remarkable and interesting as are these vital phenomena observed in roots, there is still much to be wished for in the matter of their explanation and clear comprehension. Here, as in so many similar cases, a phrase, a technical term, a word, is introduced to designate the process observed, and not infrequently

those who use it ultimately come to think they have given an explanation of the process, while really they have only stated it. This is especially the case with the term "stimulus". What is a stimulus? From the present state of our knowledge we cannot yet give a concise answer to this question, consequently explanations in which this word is inserted, are, as explanations, incomplete.

In these remarks there is no desire to depreciate the results obtained by the combined efforts of so many indefatigable investigators of past and modern times; on the contrary, we may regard the wealth of careful observations and sagacious inferences which form the present platform of our knowledge, and which have been generally reviewed in the preceding pages, with just pride and satisfaction. But this pride must not blind us to the recognition of the fact that most questions concerning the life of plants are as yet only at the commencement of their solution. Much has been done, but much is still reserved for the future.

"Manchen Flug wagt menschliches Wissen das doch
Kaum ein blatt aufschlägt in dem Buch des Weltalls."